

# Journal of Hymenoptera Research

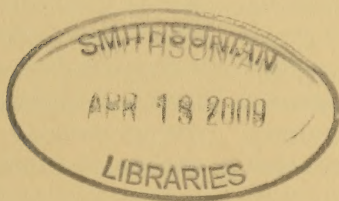
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## Structure and Functional Morphology of the Ovipositor of *Homolobus truncator* (Hymenoptera: Ichneumonoidea: Braconidae)

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**Abstract.**—The following morphological structures of the ovipositor of *Homolobus truncator* (Say) are described and hypotheses of their functions are proposed. A pre-apical notch on the exterior surface of the dorsal valve locks the ovipositor into the host cuticle. A series of sharp ridges on the distal surface of the notch helps maintain a grip on the inner surface of the host cuticle. An internal longitudinal ridge, the sperone, on the dorsal valve directs eggs away from inner surface of the ventral valves. A flap-like structure near the apex of each ventral valve covers the portal through which eggs pass and reduces evaporation of fluids in the egg canal between oviposition events. An internal hollow reservoir near the base of each ventral valve acts as a conduit to facilitate passage of fluids (venom) to more distal areas of the egg canal, where they provide hydrostatic pressure to help force eggs out of the ovipositor. An internal valve-like structure on each ventral valve, the valvillus, plays a role in maintaining egg position within the ovipositor and acts like the stopper of a hypodermic needle to push fluid against the egg and force it out of the ovipositor. Ctenidia on the inner surface of the ventral valves are instrumental in moving eggs along the basal half of the egg canal, but their role in egg movement apical to the valvillus is questionable. Ctenidia may also play a role in preventing the valvilli from scraping all fluid from the walls of the egg canal. Recurved barbs at the apex of each ventral valve hook into the inner surface of the host cuticle to maintain purchase while the thick dorsal valve is inserted. Most of these structures are widespread throughout Ichneumonoidea and our discussions are likely to pertain in whole or in part to these taxa.

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Parasitoid Hymenoptera utilize a diverse range of hosts that occupy a wide array of microhabitats. This diversity is reflected in a variety of adaptations in ovipositor morphology. Thus, ovipositor morphology can provide insights into host utilization and life history. For example, Quicke (1991) noted that the dorsal and ventral valves of *Zaglyptogastra* and *Pristomerus* varied in thickness along their length, giving the ovipositor a sinuous appearance. This characteristic allows the ovipositor to bend with differential relative positions of the dorsal and ventral valves. Quicke (1991) reasoned that this bending allows the ovipositor to navigate through

preexisting openings in the host substrate in order to locate a host. Subsequent field observations confirmed this hypothesis (Quicke and Laurenne 2005).

An understanding of functional morphology allows for inferences of biology when only morphology is known. For example, Belshaw et al. (2003) examined ovipositor characteristics of numerous Ichneumonoidea with known biologies in order to discover features that correlate with endo- or ectoparasitism. Based on these correlations they predicted the mode of parasitism of taxa using morphological data. In some instances, behavior can also be inferred from ovipositor morphology.



Lenteren et al. (1998) described the "ovipositor clip" on the dorsal valve of *Leptopilina heterotoma* (Thompson) (Hymenoptera: Figitidae) and explained how it functions to restrain the host during oviposition.

Here we describe the morphology of the ovipositor of *Homolobus truncator* (Say) and speculate on the function of numerous structures, viz., the pre-apical notch on the exterior surface of the dorsal valve; the series of sharp ridges on the distal surface of the notch; the internal longitudinal ridge, the sperone, on the dorsal valve; the flap-like structure near the apex of each ventral valve; the internal hollow reservoir near the base of each ventral valve; the ctenidia on the inner surfaces of the ventral valves; the internal valve-like structure on each ventral valve, the valvillus; and the recurved barbs at the apex of each ventral valve.

*Homolobus truncator* is a nocturnal, koinobiont, endoparasitoid of numerous species of exposed, lepidopterous larvae, primarily in the families Geometridae and Noctuidae. Among its recorded hosts are a number of economically important agricultural pests such as *Agrotis ipsilon* (Hufnagel), *Helicoverpa zea* (Boddie), *Spodoptera exigua* (Hübner), and *Spodoptera frugiperda* (Smith) (Yu et al. 2004). *H. truncator* is found in all major biotic realms except Australia (van Achterberg 1979).

## MATERIAL AND METHODS

All specimens of *H. truncator* used in this study were collected with Malaise traps in Hardy County, Virginia, USA. Species were identified using the key in van Achterberg (1979) and later confirmed by comparison with specimens of *H. truncator* determined by van Achterberg.

Specimens were stored in 95% ETOH, and dissected in the same solution. For SEM preparation, specimens were chemically dried using hexamethyldisilazane (HMDS), following the protocol of Heraty and Hawks (1998), and then coated with gold palladium. SEM images were taken

with a HitachiS-800 scanning electron microscope.

The terminology used here follows Quicke et al. (1999). Comprehensive studies of the hymenopteran ovipositor include Snodgrass (1933), Oeser (1961), Scudder (1961), Smith (1970), and Quicke et al. (1992). The muscular mechanics of hymenopteran oviposition were described by Vilhelmsen (2000).

The ovipositor is composed of a dorsal valve and paired ventral valves. The dorsal and ventral valves interlock by a 'tongue and groove' system in which each ventral valve has a longitudinal groove that interlocks with a pair of longitudinal rails (tongues) that protrude from the ventral surface of the dorsal valve. The two ventral valves are capable of sliding independently along the length of the rails of the dorsal valve (Fig. 1C). The 'tongue and groove' system is properly termed the olistheter mechanism. Together, the internal concave surfaces of the dorsal and ventral valves form the egg canal (Fig. 1C, E). These same features are ubiquitous throughout Hymenoptera with only rare exceptions.

## RESULTS AND DISCUSSION

### *Ovipositor morphology of Homolobus truncator* (Figs 1A, B, D, E, 2A–E, 3A–F, 4A–F, 5A–D)

The ovipositor of *Homolobus truncator* is short (Fig. 1A) and relatively thick and rigid except near the apices of the ventral valves (Fig. 2D, E). The dorsal valve is blunt (Fig. 1B) and contains a pre-apical notch. Immediately basal to the notch, the dorsal valve thickens to approximately twice the diameter of any point more distal (Fig. 1B, E). There are many sensory structures in this area (Figs 1B, 3E, F), which appear to be campaniform tactile sensillae (Fig. 22, 'SC' in Quicke et al. 1999). The remainder of the dorsal valve gradually increases in diameter basally.



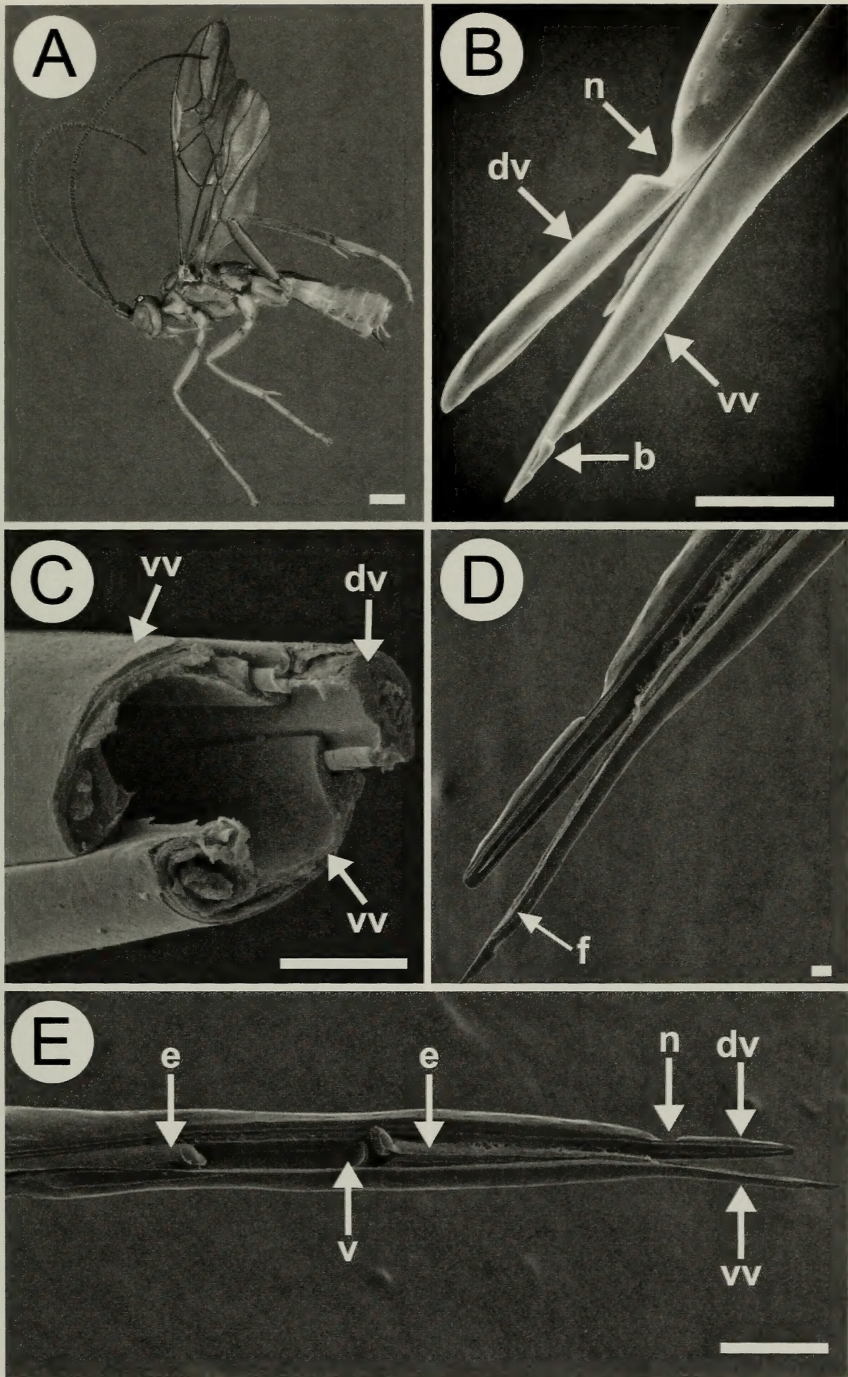


Fig. 1. A. *Homolobus truncator*: lateral habitus, scale bar = 1 mm. – B. *H. truncator*: lateral view of the distal region of the ovipositor, scale bar = 75  $\mu$ m. – C. *Meteorus* sp.: the distal region of the ovipositor is broken, scale bar = 10  $\mu$ m. – D. *H. truncator*: ovipositor apex with one ventral valve removed, arrow indicates a flap on the ventral valve, scale bar = 10  $\mu$ m. – E. *H. truncator*: lateral view of entire ovipositor with one ventral valve removed, scale bar = 100  $\mu$ m. (Abbreviations: b = barbs, dv = dorsal valve, e = egg, f = flaps, n = notch, v = valvillus, vv = ventral valve).



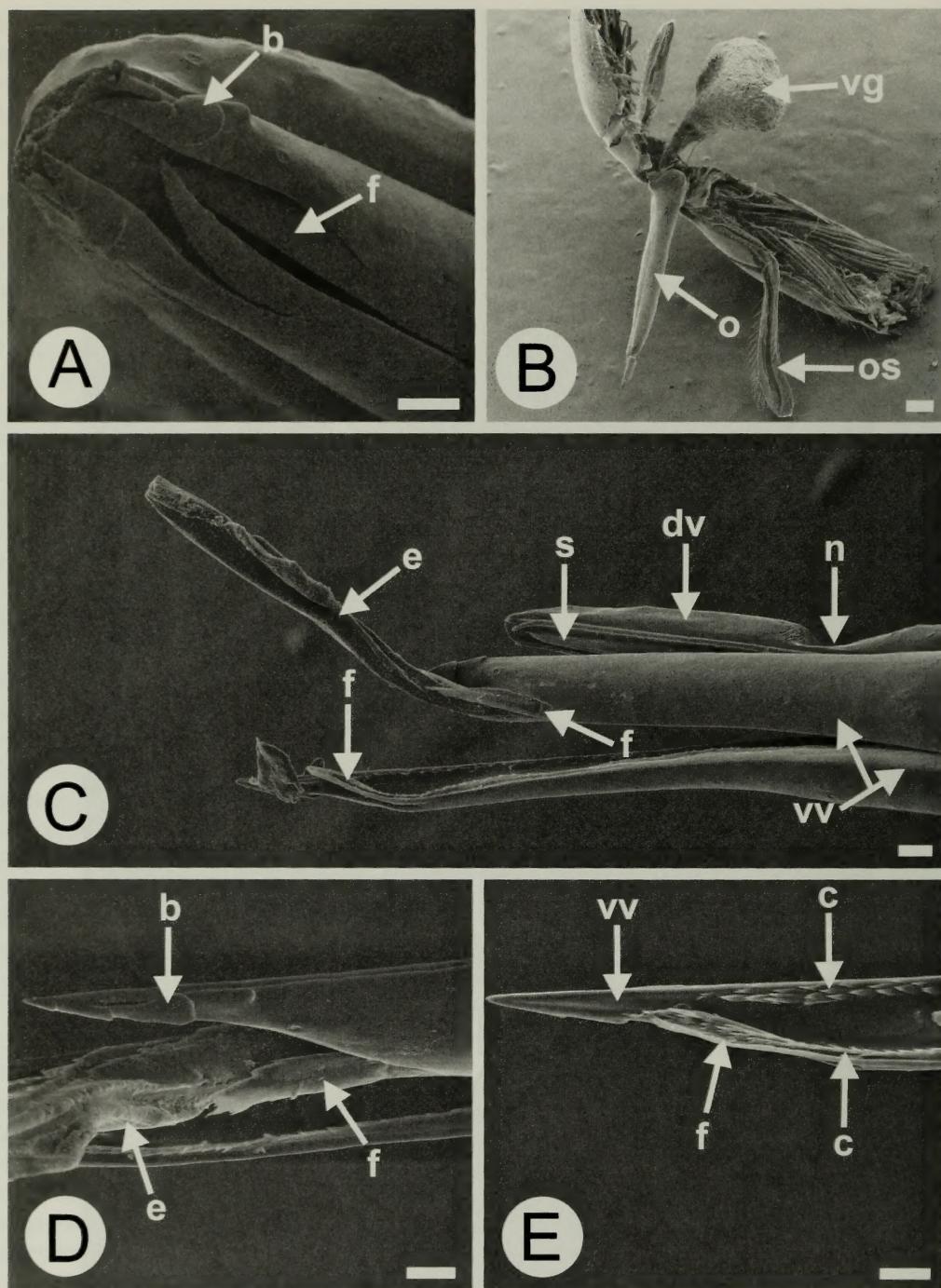


Fig. 2. A-E. *Homolobus truncator*. - A. Ventral view of the ovipositor showing a flap on each ventral valve, scale bar = 10  $\mu$ m. - B. View of the entire ovipositor and venom gland, scale bar = 100  $\mu$ m. - C. Latero-ventral view of the ovipositor with an egg exiting from the flap on the ventral valve, scale bar = 10  $\mu$ m. - D. Lateral view of the exterior ventral valve with an egg exiting from the flap on the ventral valve, scale bar = 10  $\mu$ m. - E. Lateral view of the interior ventral valve, scale bar = 10  $\mu$ m. (Abbreviations: see Fig. 1, c = ctenidia, o = ovipositor, os = ovipositor sheath, s = sperone, vg = venom gland).



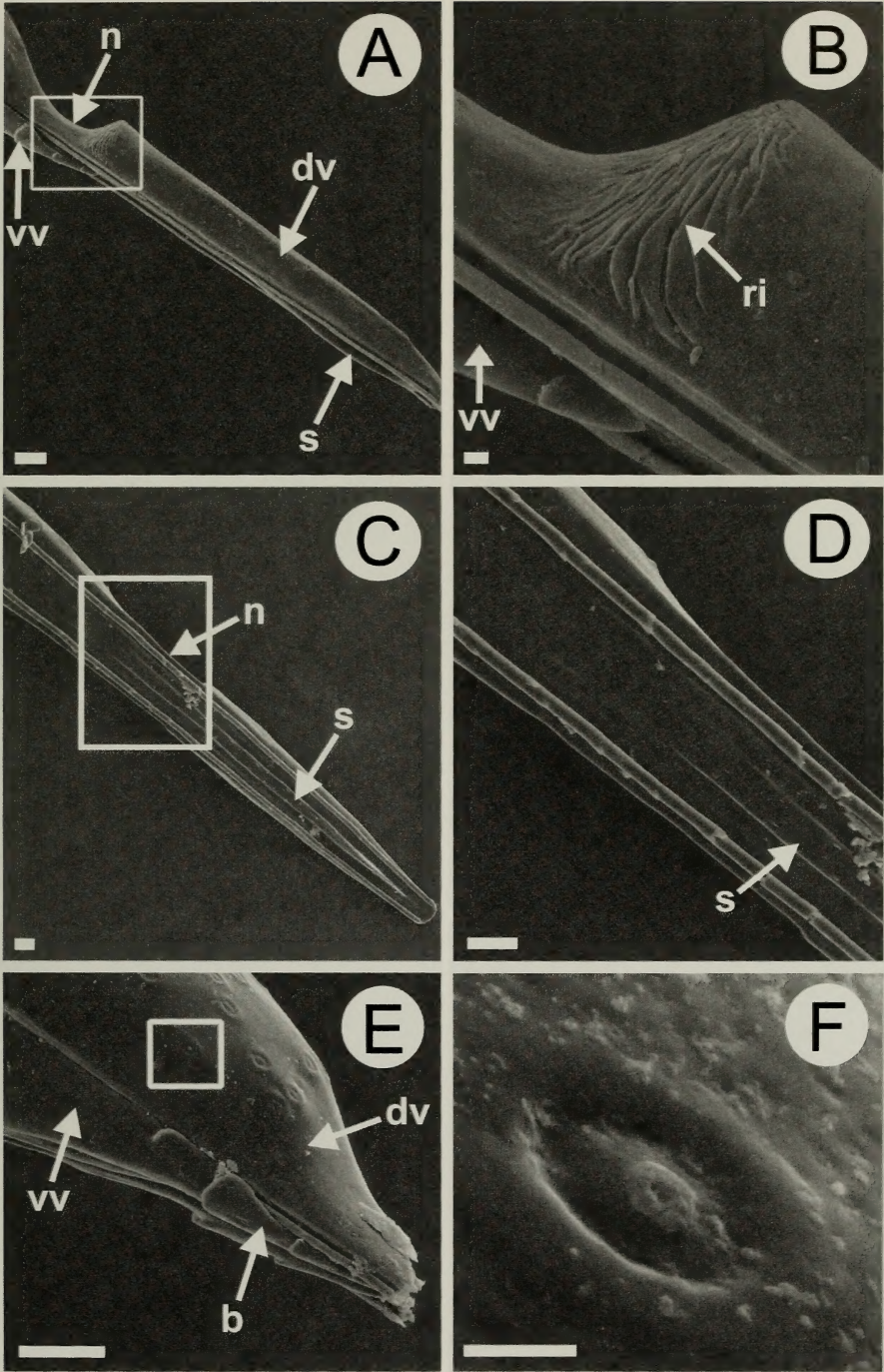


Fig. 3. A–F. *Homolobus truncator*. – A. Lateral view of the ovipositor with a rectangle outlining the location of Fig. 3B, scale bar = 10  $\mu$ m. – B. High magnification of the outlined region in Fig. 3A, scale bar = 1  $\mu$ m. – C. Ventral view of the dorsal valve with a rectangle outlining the location of Fig. 3D, scale bar = 10  $\mu$ m. – D. High magnification of the outlined region in Fig. 3C, scale bar = 10  $\mu$ m. – E. Lateral view of the ovipositor with the tip broken at the notch. The rectangle outlines the sensory structure in Fig. 3F, scale bar = 1 mm. – F. High magnification of the outlined region in Fig. 3E, scale bar = 1  $\mu$ m. (Abbreviations: see Fig. 1 and Fig. 2, ri = ridges).



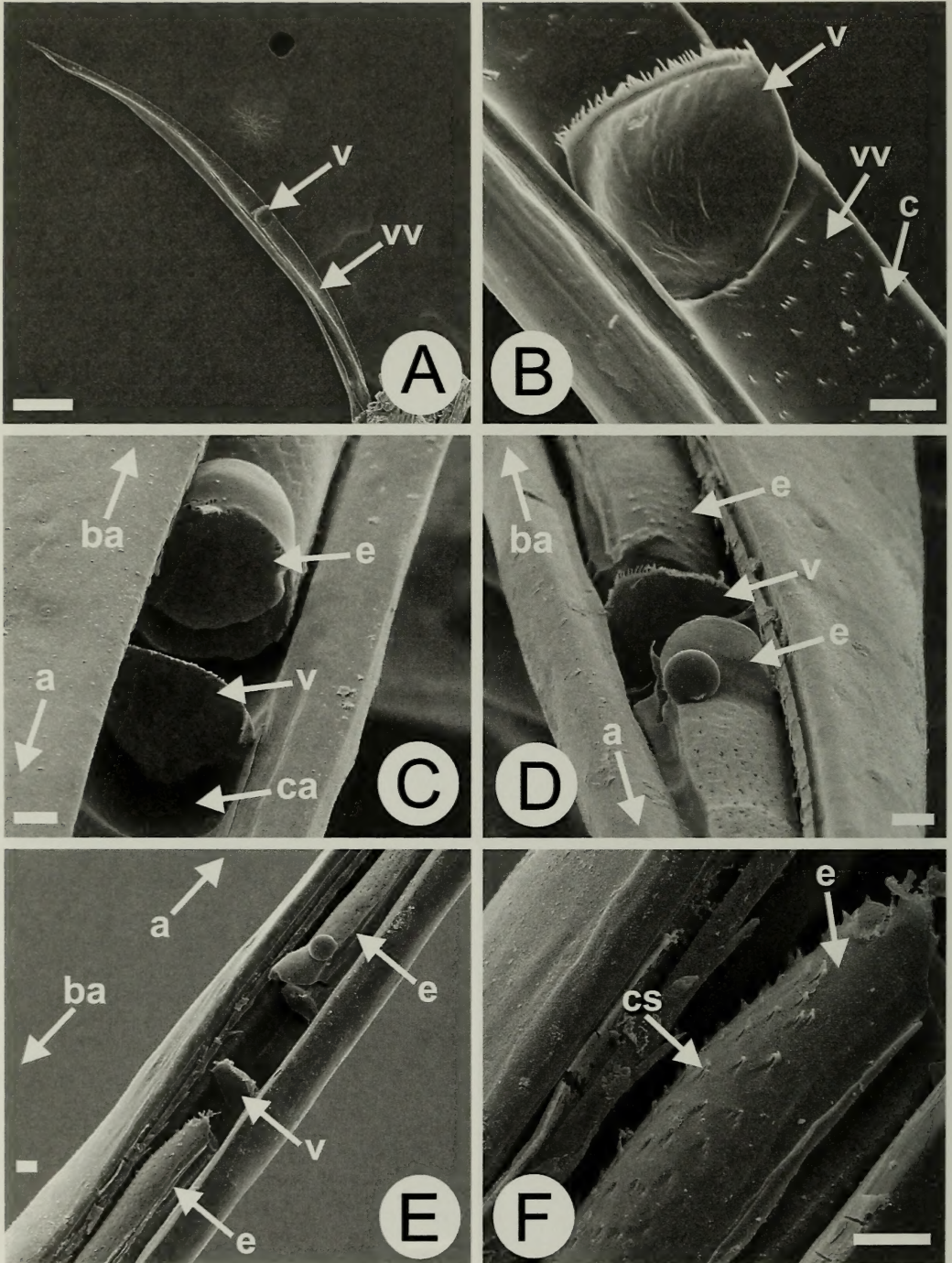


Fig. 4. A-F. *Homolobus truncator*. - A. Lateral view of the ventral valve interior, scale bar = 100  $\mu\text{m}$ . - B. The valvillus, scale bar = 10  $\mu\text{m}$ . - C. Lateral view of the ovipositor with one ventral valve removed, scale bar = 10  $\mu\text{m}$ . - D. Lateral view of the ovipositor with one ventral valve removed, scale bar = 10  $\mu\text{m}$ . - E. Lateral view of the ovipositor with one ventral valve removed, scale bar = 10  $\mu\text{m}$ . - F. Lateral view of the ovipositor with one ventral valve removed showing high magnification of an egg in the egg canal, scale bar = 10  $\mu\text{m}$ . (Abbreviations: see Fig. 1 and Fig. 2, a = apical direction of ovipositor, ba = basal direction of ovipositor, ca = cavity for valvillus, cs = ctendial scars).



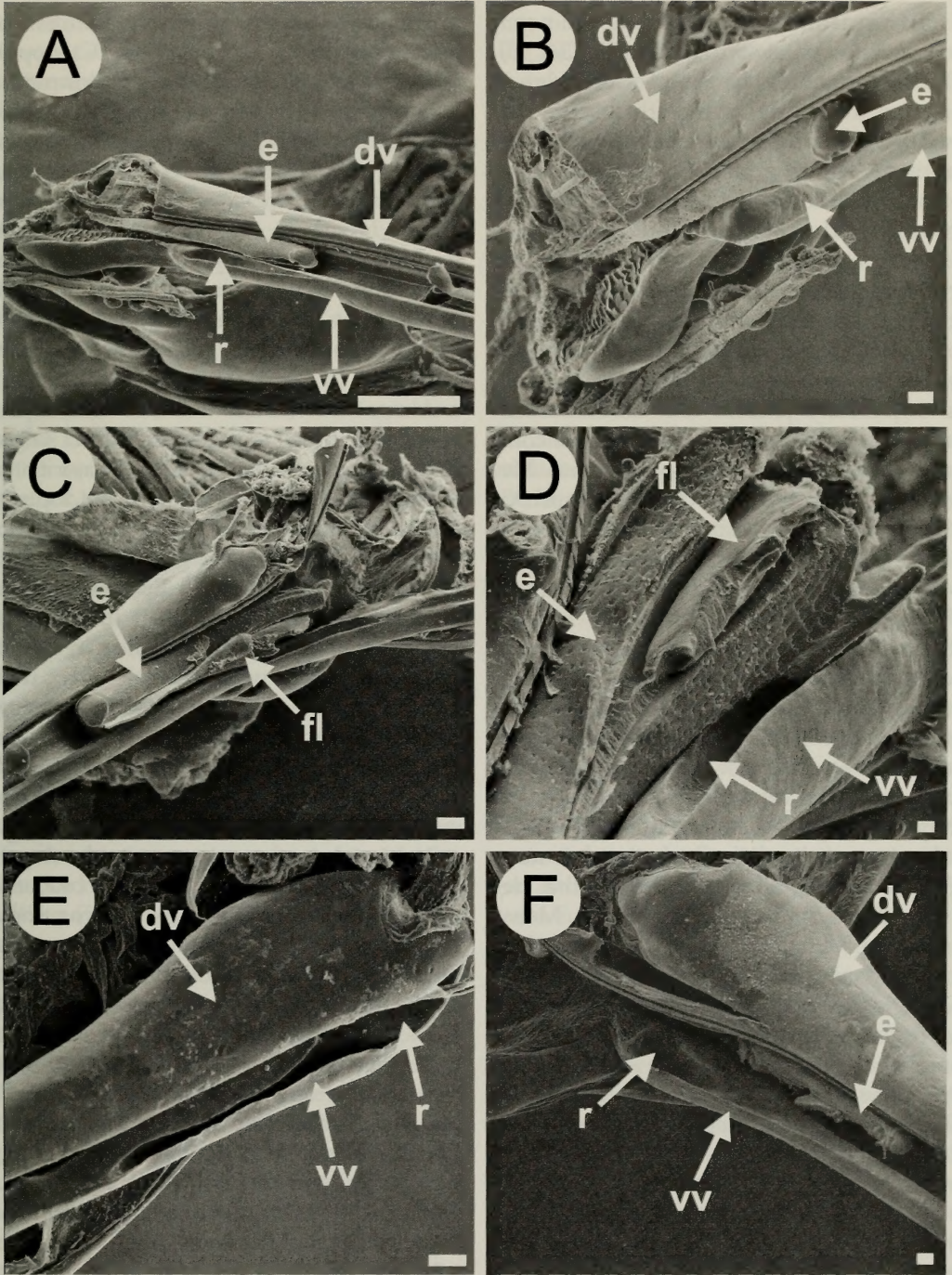


Fig. 5. A–D. – A. *Homolobus truncator*: Latero-ventral view of the ovipositor with one ventral valve removed, scale bar = 100 μm. – B. *Homolobus truncator*: Lateral view of the ovipositor with one ventral valve removed, scale bar = 10 μm. – C. *Homolobus truncator*: Latero-ventral view of the ovipositor with one ventral valve removed, scale bar = 10 μm. – D. *Homolobus truncator*: Latero-ventral view of the ovipositor with one ventral valve removed, scale bar = 10 μm. – E. Blacinae: lateral view of the ovipositor base with one ventral valve removed, scale bar = 10 μm. – F. *Austrozele* sp. (Macrocentrinae): Latero-ventral view of the ovipositor with one ventral valve removed, scale bar = 10 μm. (Abbreviations: see Fig. 1, fl = congealed fluid, r = reservoir).



The distal surface of the pre-apical notch has a series of sharp ridges (Fig. 3A, B). The scarp (acute) surface of each ridge is directed anteriorly. Although we did not quantify the ridges, the peak-to-peak separation of the ridges is approximately 1  $\mu\text{m}$ , and the peak-to-valley height is a few hundred nanometers.

The pre-apical notch is widespread in Ichneumonoidea. It is clear that at least some occurrences of the ovipositor notch are convergent. Braconid subfamilies where the pre-apical notch is commonly or universally present are: Amicrocentrinae, Charmontinae, Euphorinae, Helconinae, Homolobinae, Macrocentrinae, Meteorinae, Microtypinae, Orgilinae, and Xiphozelinae. Presence of a pre-apical notch is rare in the braconid subfamilies Cardiochilinae and Cenocoeliinae. When present in the Cenocoeliinae, the notch is very shallow. The frequency of the pre-apical notch in Aphidiinae and Blacinae is unknown; in both subfamilies there are species with and without the pre-apical notch but we have not surveyed sufficiently to provide reasonable estimates. The shape of the pre-apical notch in Aphidiinae is fundamentally different in that it is not a simple indentation but rather the depressed area is relatively quite long. Many, or perhaps most, Alysiinae have a structure that appears much like a pre-apical notch which may even function in certain aspects like those of the aforementioned braconids. In members of the Alysiinae, the tip of the dorsal valve is swollen and the diameter decreases rapidly; however this decrease in diameter remains relatively constant toward the base, though it gradually thickens. The structure at the apex of the dorsal valve in Alysiinae may be a modified nodus. We were unable to find a pre-apical notch in any ichneutine genera including *Ichneutes*, although Rahman et al. (1998, char. N) coded the pre-apical notch present for Ichneutinae (*Ichneutes* sp.). Ichneumonid subfamilies where the pre-apical notch is commonly or universally

present are: Anomaloninae, Banchinae, Campopleginae, Cremastinae, Ctenopelmatinae, Neorhacodinae, Ophioninae, Oxytorinae, Tatogastrinae, and Tersilochinae (David Wahl, *pers. comm.*). Approximately half of the genera in Metopiinae and Orthocentrinae possess a pre-apical notch. However, the notch tends to be shallow to moderately shallow when present. Although most members of Stilbopinae do not possess a pre-apical notch, it can be found in *Notostilbops fulvipes* Townes.

Almost all ichneumonoids with a pre-apical notch are endoparasitoids of larval holometabolous insects. The majority of these ichneumonoids attack Lepidoptera, but some attack larval Diptera or Coleoptera. Exceptions to these generalities can be found in many genera of Euphorinae that are endoparasitoids of adult insects. The presence of a pre-apical notch is not constrained by ovipositor length; it is found in species with long ovipositors that probe deep into substrates such as wood and leaf-rolls, as well as in species with short ovipositors that oviposit directly into exposed hosts. We did not observe a pre-apical notch in any ectoparasitoids. A pre-apical notch was absent in all braconid cyclostome subfamilies, except for some Aphidiinae. We did not detect a pre-apical notch in any of the following non-cyclostome subfamilies: Adeliinae, Agathidinae, Cheloninae, Ichneutinae (however see Rahman et al. 1998, char. N), and Sigalphinae. The endoparasitoid subfamilies Agathidinae and Sigalphinae are peculiar amongst the Braconidae in that they deposit the egg in a ganglion of the host (Shaw and Quicke 2000) and therefore very precise deposition is necessary. Members of Cheloninae, which oviposit in the eggs of their hosts and emerge from the larvae, do not have a pre-apical notch, and this may be true for all egg-larval ichneumonoid parasitoids, though we have not conducted a detailed survey. Within the Ichneumonidae, some Stilbopinae (*Stilbops* spp.) are egg-larval



parasitoids, and these species also lack a pre-apical notch. Only one species of Stilbopinae, *Notostilbops fulvipes*, has a pre-apical notch and the biology of this rare species is unknown. It is unreasonable to assume that *N. fulvipes* is an egg-larval parasitoid since some other Stilbopinae (*Panteles schuetzeanus* (Roman)) are endoparasitoids of Lepidoptera larvae (Quicke 2005).

There is a well-developed sperone, an internal median longitudinal ridge, near the apex of the ventral surface of the dorsal valve (Figs 1D, 3A, C, D). The sperone begins immediately basal to the pre-apical notch and is most pronounced near the apex of the dorsal valve where it projects into the egg canal. Rahman et al. (1998, characters O, P) surveyed the distribution of the sperone and pre-apical notch in the Braconidae, as did Quicke and Belshaw (1999, chars. 52, 53). These studies reported that a sperone is present in many non-cyclostome Braconidae, as well as in the ichneumonid *Xorides*. Both studies demonstrated an association between the pre-apical notch and the sperone in that all taxa with a pre-apical notch also had a sperone. However, a sperone may be present in the absence of a pre-apical notch, e.g. *Trioxys pallidus* (Haliday).

The two ventral valves of *H. truncator* narrow toward the apices and are sharply pointed. Each valve has a small series of recurved barbs near the apex (Fig. 2D), which are ubiquitous across Hymenoptera. On the outer (ventral surface), there is a flap-like structure on each valve, immediately basal to the apex (Fig. 2A) and mesal to the barbs. Rahman et al. (1998, character N) examined the distribution of the flap-like seal within the Braconidae and found it absent in all cyclostome taxa and present in the majority of non-cyclostome braconids. We examined those non-cyclostome braconids coded by Rahman et al. (1998, character N) as absent and found this feature present in *Eubazus* (Fig. 6A), Macrocentrinae (Fig. 6C), and Euphorinae

(Fig. 6B). The subfamilies Microgastrinae (Fig. 6D) and Meteorinae (Fig. 6E) appear to be the only non-cyclostome subfamilies without flap-like structures on the apex of the ventral valves, however denser taxon sampling is needed to make a firm conclusion. Other microgastrid subfamilies and Euphorinae genera have the flap-like structure present. We suggest these flap-like structures are a putative synapomorphy of the non-cyclostome Braconidae.

The ventral valves quickly increase in diameter and then remain relatively constant in diameter toward their bases. The surface of the egg canal of most hymenopterans and many other insects is covered with scattered ctenidia or scales that are set almost flat against the surface with the basal end attached and the distal end free (Smith 1968; Austin and Browning 1981; Rahman et al. 1998). In specimens of *H. truncator* the ctenidia are absent from the dorsal valve except for a small number present on the sperone. The ctenidia on the ventral valves are scattered over most of the inner surface, except near the apex where they are absent medially and concentrated marginally, where they are longer and less rigid (Figs 2E, 4A). The egg canal narrows considerably near the apex of the ovipositor.

Internally, near mid-length, each ventral valve has one chitinous valvillus (Fig. 4A–E). The valvilli rotate over a 90° arc; from perpendicular to the egg canal axis to parallel with the axis and directed apically. The ovipositor valvilli have no intrinsic musculature, therefore the movement of the valvilli is controlled by the relative motion of the valves and perhaps by fluid pressure in the egg canal. Each valvillus is margined by a narrow but dense fringe (Fig. 4B). The valvillus is deeply imbedded within the wall of the egg canal, and immediately apical to the valvillus the egg canal is excavated to allow the valvillus to lay flat (Fig. 4C). When a valvillus is perpendicular and blocking the egg canal,



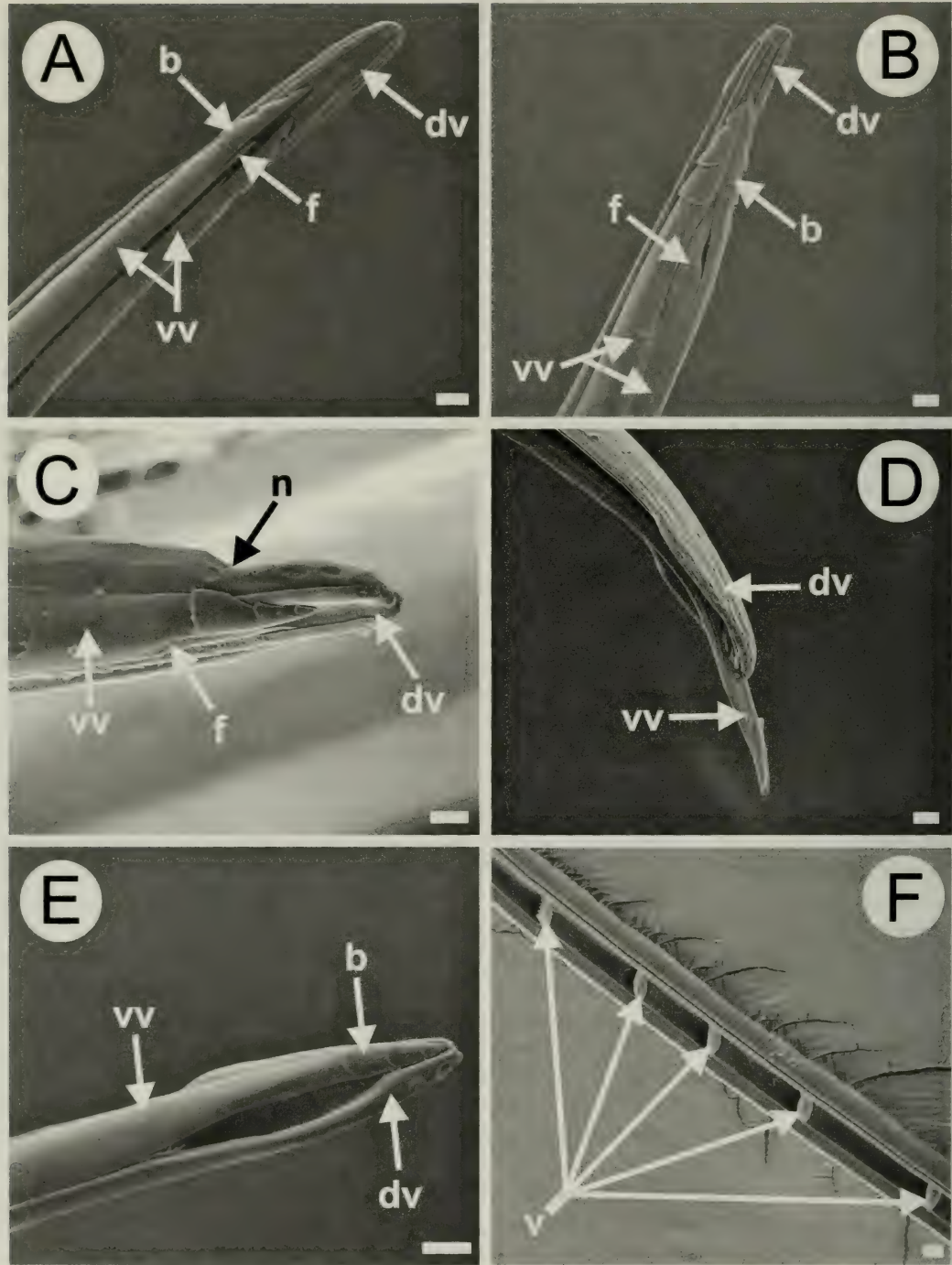


Fig. 6. A. *Eubazus* (Helconinae): ventral view of the ovipositor apex, scale bar = 10 µm. – B. *Strebloclera* (Euphorinae): ventral view of the ovipositor apex, scale bar = 10 µm. – C. Macrocentrinae: latero-ventral view of the ovipositor apex, scale bar = 10 µm. – D. Microgastrinae: lateral view of the ovipositor apex with one ventral valve removed, scale bar = 10 µm. – E. *Meteorus* (Meteorinae): ventral view of the ovipositor apex with one ventral valve removed, scale bar = 10 µm. – F. *Wroughtonia* sp. (Helconinae): lateral view of the ovipositor with one ventral valve removed, scale bar = 10 µm. (Abbreviations: see Fig. 1).



it appears to be of a shape and size capable of sealing the egg canal (Fig. 4C, D)

An internal, excavated reservoir near the base of each ventral valve (Fig. 5A–D) is described here for the first time. It is approximately 170  $\mu\text{m}$  long, 20  $\mu\text{m}$  wide at the base, and it tapers to a point apically. It appears to be about as deep as it is wide (Fig. 5A, B). A preliminary survey of braconid subfamilies found this feature to be present in Blacinae (Fig. 5E), Helconinae (*Wroughtonia* sp.), Homolobinae, Meteorinae (*Zeke* sp.), and Macrocentrinae (*Austrozele* sp.) (Fig. 5F). The reservoir is well developed in *Homolobus* and least developed in *Wroughtonia* and *Zeke*. We did not find a reservoir present in Agathidinae, Braconinae, Doryctinae, Rogadinae, or *Campoletis sonorensis* (Cameron) (Ichneumonidae). The reservoir may represent a synapomorphy for a subset of non-cyclostome braconids, but obviously more taxon sampling is needed to test this idea.

### Functional morphology

Our hypotheses on the functions of various ovipositor structures are based on careful examination of morphological structures. Direct observations are difficult because most of the events that we postulate take place inside the host or inside the ovipositor. The strengths, and weaknesses, of the hypotheses are based primarily on their explanatory power, i.e., their power to explain the morphology of the observed structures in a parsimonious and logical manner. In some cases arguments may be convincing, and in other cases we are offering what amounts to little more than speculation.

In the following paragraphs hypotheses on the oviposition process in *H. truncator* are broken down into four phases: penetration of the host cuticle, locking mechanism, egg movement, and egg-laying and ovipositor withdrawal. A concise overview is presented in the next paragraph and illustrated in Fig. 8. In Fig. 8, the host cuticle is represented by a horizontal black

line. The dorsal valve is light grey and on the right. On the left there are two ventral valves, one is light grey and in the foreground, the other is dark grey and in the background. The arrows on the left indicate the movement of the ventral valves; the color of the arrow corresponds to the movement of the valve with the same color. An arrow on the right indicates movement of the dorsal valve. In Fig. 8F, the dark grey ventral valve moves upward as indicated by the dark grey arrow; this movement is visually obstructed by the light grey ventral valve in the foreground because the dark grey ventral valve is in the background. This visual obstruction also occurs in Fig. 8M, N, Q, and R. The valvilli are represented by horizontal ovals, where the dark grey valvillus is attached to the dark grey ventral valve and the light grey valvillus is attached to the light grey ventral valve. When the valvillus is represented by a thin oval, the valvillus is perpendicular and blocks the egg canal. When the valvillus is represented by a large oval, the valvillus is parallel to, and allows movement through the egg canal. In Fig. 8H, venom enters the egg canal, which is represented by the color yellow. The egg is represented by the white, vertical oval. In Fig. 8O, the egg begins to exit the ovipositor from a flap on the ventral valve. In Fig. 8R the egg is visually obstructing the flap.

Before a host is encountered, the egg is positioned near the tip of the ovipositor (see later). It is held in place basally by the valvilli and apically by the narrow apex of the egg canal and the sperone, which blocks the aperture of the egg canal. The tip of the ovipositor comes into contact with the host cuticle with all three valves aligned apically and flush with the surface of the host cuticle (Fig. 8A). The sharp ventral valves penetrate the host cuticle (Fig. 8B, C) to a depth sufficient to create a relatively large wound (Fig. 8D, E). The ventral valves are then partially withdrawn to the point where their sharp barbs



engage the internal surface of the host cuticle (Fig. 8F). At this time the blunt dorsal valve is pushed into the newly formed wound. The dorsal valve enters the host until the pre-apical notch slips onto the host integument (Fig. 8G, H). The ventral valves are then reinserted and egg-laying is effected with a series of alternating thrusts of the ventral valves (Fig. 8I–T). Although the egg is positioned at the apex of the ovipositor by movement of the ventral valves and the gripping force of the ctenidia, we speculate that once the egg is past the valvilli, further movement of the egg is facilitated by the valvilli pushing venom against the egg. On its way to the ovipositor apex, friction of the egg against the sperone forces the egg through the flaps in the ventral valves (Fig. 8O–Q). As the egg emerges from the ovipositor, elastic energy stored in the chorion provides additional force to help move the egg out of the ovipositor (Fig. 8R, S).

*Phase 1: Ovipositor penetration of the host cuticle.*—We postulate that the dorsal and ventral valves contact the host cuticle in unison with an egg positioned near the tip of the ovipositor (Fig. 8A). Contact with either one of the valves independently would cause unnecessary risk of fracturing one of the valves as both appear to be relatively fragile by virtue of their small cross-sectional area and barbs which act as stress raisers. The sharp ventral valves then penetrate the host (Fig. 8B, C) and are pushed deeply into the host to create a wound sufficiently large to facilitate entry of the relatively blunt dorsal valve (Fig. 8D–H). This explains the sharp points of the ventral valves and the rapid increase in the diameter of the ventral valves near the apex. It is uncertain if the ventral valves thrust in unison or in opposition; video of wood-boring ectoparasitic Ichneumonidae shows the ventral valves moving in opposition (Skinner and Thompson 1960). For this reason, Fig. 8 shows the ventral valves thrusting in opposition, however it is not beyond reason that the ventral valves

move in unison. One exception is shown in Fig. 8F where the ventral valves are withdrawn in unison. This is necessary to prevent damaging the egg (see below). After penetration, we posit that the ventral valves are withdrawn to the point where the recurved barbs hook onto the inner surface of the host cuticle (Fig. 8F). At this point the wound is much larger than the diameter of the apical portion of the ventral valves that occupy it, thereby leaving room for the thick dorsal valve to enter. If the ventral valves were deeply inserted while the blunt dorsal valve was entering the host, the resulting wound would be excessively large and this would impede the effectiveness of the locking mechanism (see below).

*Phase 2: Locking mechanism.*—Belshaw et al. (2003) stated that the “pre-apical notch in the upper valve is tentatively assumed to be associated with moderating penetration of the host cuticle...” (p. 217) and van Veen (1982) observed that the ovipositor of *Banchus femoralis* Thomson is inserted into the host cuticle no further than the notch. Little else has been mentioned in the literature concerning this ubiquitous modification of the ovipositor. We suggest that the function of the notch is two-fold; it is part of a temporary locking mechanism that ensures continuous engagement with the host during oviposition, and in agreement with van Veen (1982), we suggest that it facilitates the correct depth of ovipositor penetration.

After initial penetration, the dorsal valve is pushed into the host until the host cuticle comes in contact with the base of the notch (Fig. 8G, H). This region is covered in campaniform sensillae (Fig. 3E, F) which we presume signal the wasp to stop thrusting the dorsal valve. After the cuticle of the host slips onto the notch on the dorsal valve, we posit that the ventral valves are pushed further into the host to a point where the thick section of the ventral valves align across from the dorsal notch (Fig. 8I–L). At this point, the notch,



and all other surfaces of the ovipositor, would be pressed firmly against the host cuticle, effectively locking the ovipositor into the host. During oviposition the ventral valves move in opposition to one another to effect movement of the egg (see below). During this activity the pressure between the exoskeleton of the host and the ovipositor remains constant because the diameter of the parts of the ventral valves that come into contact with the host cuticle is uniform (Fig. 8K–N). During the process of locking into the host cuticle, Fig. 8E, F, we suggest that the ventral valves must be withdrawn in unison, either directly or indirectly through abdominal movement. If the ventral valves withdraw in opposition to each other in Fig. 8E, F, their ctenidia would resist proximal movement of the egg toward the valvelli. If the ventral valves move in unison, the egg would remain supported by the ventral valves. Since the dorsal valve lacks ctenidia proximal to the notch, movement of the ventral valves in unison would not damage or cause distal movement of the egg.

Sharp transverse ridges are located over the distal surface of the pre-apical notch (Fig. 3A, B). This is the area of the dorsal valve in contact with the inner surface of the host cuticle. The sharp surfaces of the ridges face anteriorly and appear to be able to efficiently grip the inner surface of the host cuticle by creating numerous shallow penetrations. The sharp ridges and the resulting reduction in contact area would result in greater traction to be applied to the inner surface of the host's cuticle, much like the jaws of a pipe wrench. We have not conducted a systematic survey across the Ichneumonoidea for this feature.

Quicke et al. (1999) speculated that the pre-apical notch might be a point of articulation, "as if the tip might be able to hinge upwards, perhaps to assist exit of the egg." (p. 204). There are several reasons why we think that this is not likely to be the case in *H. truncator*. First, this scenario necessitates that the olistheter mechanism

be derailed and it is hard to imagine a method to re-couple the interlocked dorsal and ventral valves (Fig. 1C), especially if they are not parallel to each other. Secondly, the idea lacks explanatory power in that if the dorsal and ventral valves were not in contact during oviposition it fails to explain the function of the sperone and the flaps near the apices of the ventral valves (see below)

*Phase 3: Mechanism of egg movement along the egg canal.*—Ctenidia on the surface of the egg canal in Hymenoptera and other insects are thought to act like stiff brushes to grip and push the egg down the canal and to prevent backward movement of the egg. In his study of the common black field cricket, *Gryllus assimilis* (Fabricius), Severin (1935) observed a direct correlation between alternating valve thrusts and movement of the egg through the ovipositor. Austin and Browning (1981) confirmed that the alternating action of the valves is responsible for egg movement in the gryllid *Teleogryllus commodus* (Walker) by directly manipulating the valves of anaesthetized specimens with fine forceps. It has also been shown that the egg is moved down the canal with alternating thrusts of the two ventral valves in some Hymenoptera. Cole (1981) observed specimens of the ichneumonid parasitoid *Itopectus maculator* (Fabricius) ovipositing into the lepidopterous hosts *Galleria mellonella* (Linnaeus) and *Ephesia kuehniella* (Zeller). He noted that the ventral valves moved rhythmically back and forth after the ovipositor was inserted into the host. He also demonstrated that the egg must move down the egg canal after the ovipositor was inserted into the host because the parasitoids were capable of selecting the sex of their offspring, an action that logically follows contact and assessment of the host with the ovipositor.

The ctenidia of *H. truncator* are involved in egg movement in the basal half of the egg canal. Fig. 4E shows an egg of a specimen of *H. truncator* positioned near



the base of the egg canal. The surface of the egg is marked with indentations and small scars caused by contact with ctenidia. To create these scars, ctenidia of the ventral valves must have been firmly imbedded into the surface of the egg and any apical movement of the valves would necessarily result in a corresponding movement of the egg.

The fact that many aculeates (e.g. Fig. 7C, D) have ctenidia on some parts of the inner surface of the sting suggests that, at least for these species, the ctenidia have functions other than gripping and pushing eggs. The diverse morphology of ctenidia across Hymenoptera also implies multiple functions. We suggest that, besides moving eggs along the egg canal, the ctenidia may decrease friction by aiding lubrication. Ctenidia may also help to maintain a minimal amount of liquid in the egg canal. When one ventral valve moves apically relative to the other ventral valve, the valvillus of the former rubs against the inner surface of the latter. If the walls lacked ctenidia, all liquids, some of which may have a lubricating function (Bender 1943; Robertson 1968) would be scraped away. It stands to reason that the small separation of the ctenidia from the egg canal wall could act as a miniscule fluid reservoir whereby wetting of the fluid into the gap would result in some fluid retention surrounding the ctenidia, thus improving lubricity. Conceivably, this would make it easier for eggs to pass by decreasing frictional forces against the egg canal wall via the action of lubricating fluid. In the "venom canal" of *Vespa crabro* Linnaeus, thick ctenidia similar to those found in the egg canals of parasitoids are found only on the dorsal valve (Fig. 7C, D). Further research is necessary to test these conjectures.

Although there is convincing evidence showing that ctenidia, in conjunction with alternating thrusts of the ventral valves, move the egg along the basal portion of the egg canal, we suggest that the valvilli may

assist movement of the egg in the distal half of the egg canal. Ichneumonoids and aculeate Hymenoptera are unique among Hymenoptera in that many members possess valvilli (Figs 4A–F, 7A, B). These are valve-like structures in the ventral ovipositor valves that are able to block the egg canal; in the ichneumonidea there are typically one pair per ventral valve but there may be as many as 5, as for example in *Wroughtonia* sp. (Fig. 6F). Because the aculeate sting does not function as an egg-laying device, the valvilli of aculeates are almost certainly employed as valves to pump venom into their hosts and/or potential predators (Janet 1898; Snodgrass 1925, 1956; Marle and Piek 1986). Rogers (1972), in his study of the ichneumonid endoparasitoid *Venturia canescens* (Gravenhorst), suggested that the valvillus functions to maintain the egg in place near the apex of the ovipositor. Quicke et al. (1992), noting the different uses of the ovipositor in aculeates and parasitoids, suggested that valvilli may have different functions in the two groups; presumably they meant egg positioning in parasitoids and venom injection in aculeates.

Figure 1E shows the ovipositor of *H. truncator* with the right ventral valve removed. Two eggs are visible in the egg canal. One is situated basally and the other is positioned near the apex with its basal end abutting the valvillus and its distal end aligning with the notch on the dorsal valve and the point where the ventral valve narrows. We suggest that this is the typical position of an egg ready for oviposition. We dissected numerous ovipositors of *H. truncator* and, with few exceptions we found an egg in this apical position. One exception is illustrated in Figures 2C and 2D, where the apical end of an egg may be seen extruding from the flap-like structures near the apex of the ventral valves. The "loaded" egg position is undoubtedly obtained with alternating thrusts of the lower valves in conjunction with friction provided by the apically directed ctenidia.



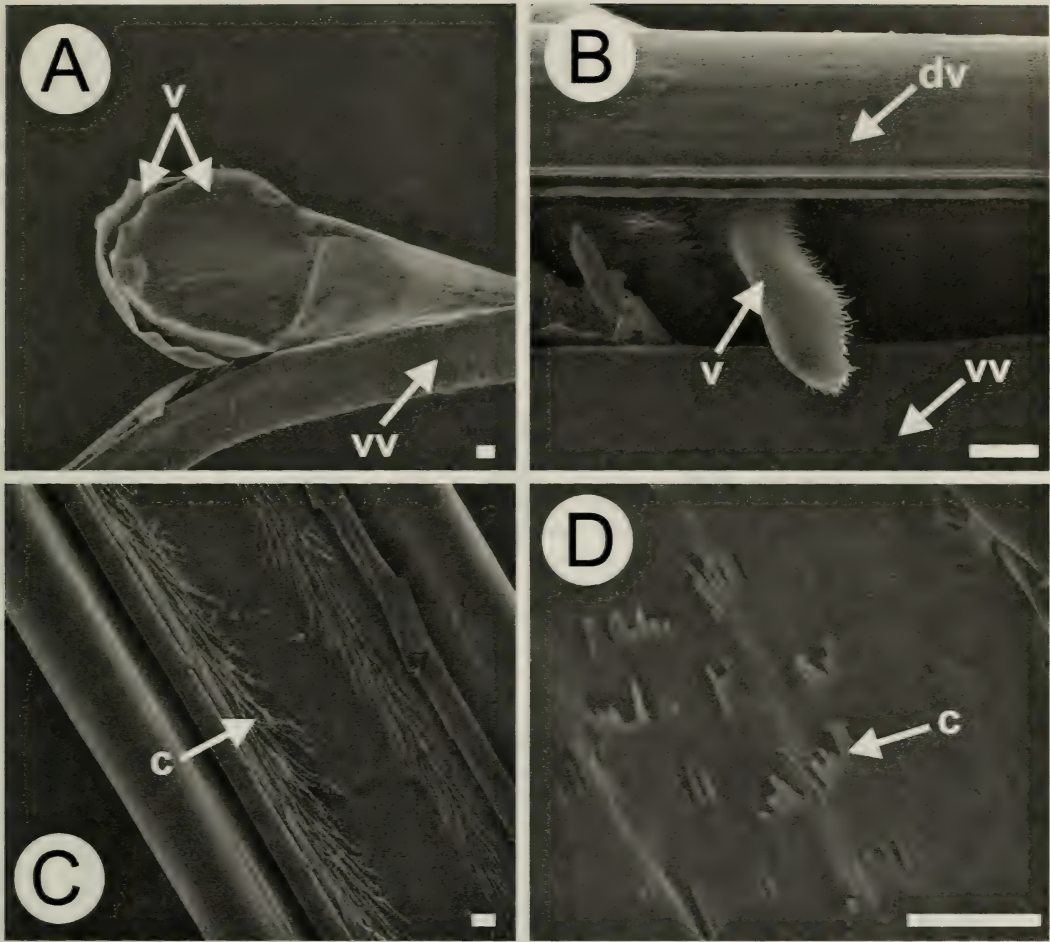


Fig. 7. A. *Sphex nudus* (Sphecidae): lateral view of the valvilli (2 valvilli lay side-by-side in all aculeates with valvilli), scale bar = 10  $\mu$ m. – B. *Campoletis sonorensis* (Ichneumonidae): lateral view of the valvillus, scale bar = 10  $\mu$ m. – C. *Vespa crabro* (Vespidae): ventral view of dorsal valve showing ctenidia near ovipositor apex, scale bar = 10  $\mu$ m. – D. *Vespa crabro* (Vespidae): ventral view of dorsal valve showing ctenidia near ovipositor base, scale bar = 10  $\mu$ m. (Abbreviations: see Fig. 1 and Fig. 2).

In agreement with Rogers (1992), it appears that one function of the valvillus in *H. truncator* appears to be to lock the egg into this loaded position. This is clearly not the case in all ichneumonoids, because, as mentioned previously, Cole (1981) showed that the egg of *Itopectus maculator* must move down the entire length of the egg canal after the ovipositor is inserted into the host. If Rogers (1992) and we are correct, then unlike that of *I. maculator*, the sex of the eggs of *H. truncator* is determined before contact with the host.

The phylogenetic positions of Aculeata and Ichneumonoidea among the apocritan Hymenoptera are controversial; however they are usually thought to be sister-groups (Rasnitsyn 1988; Dowton et al. 1997; Ronquist et al. 1999). The putative morphological synapomorphies supporting this relationship are the shape of the metasomal-propodeal articulation and the presence of valvilli (Mason 1983; Rasnitsyn 1988). The presence of valvilli is clearly ground-plan for both taxa. We know that the function of the valvilli of aculeates is to



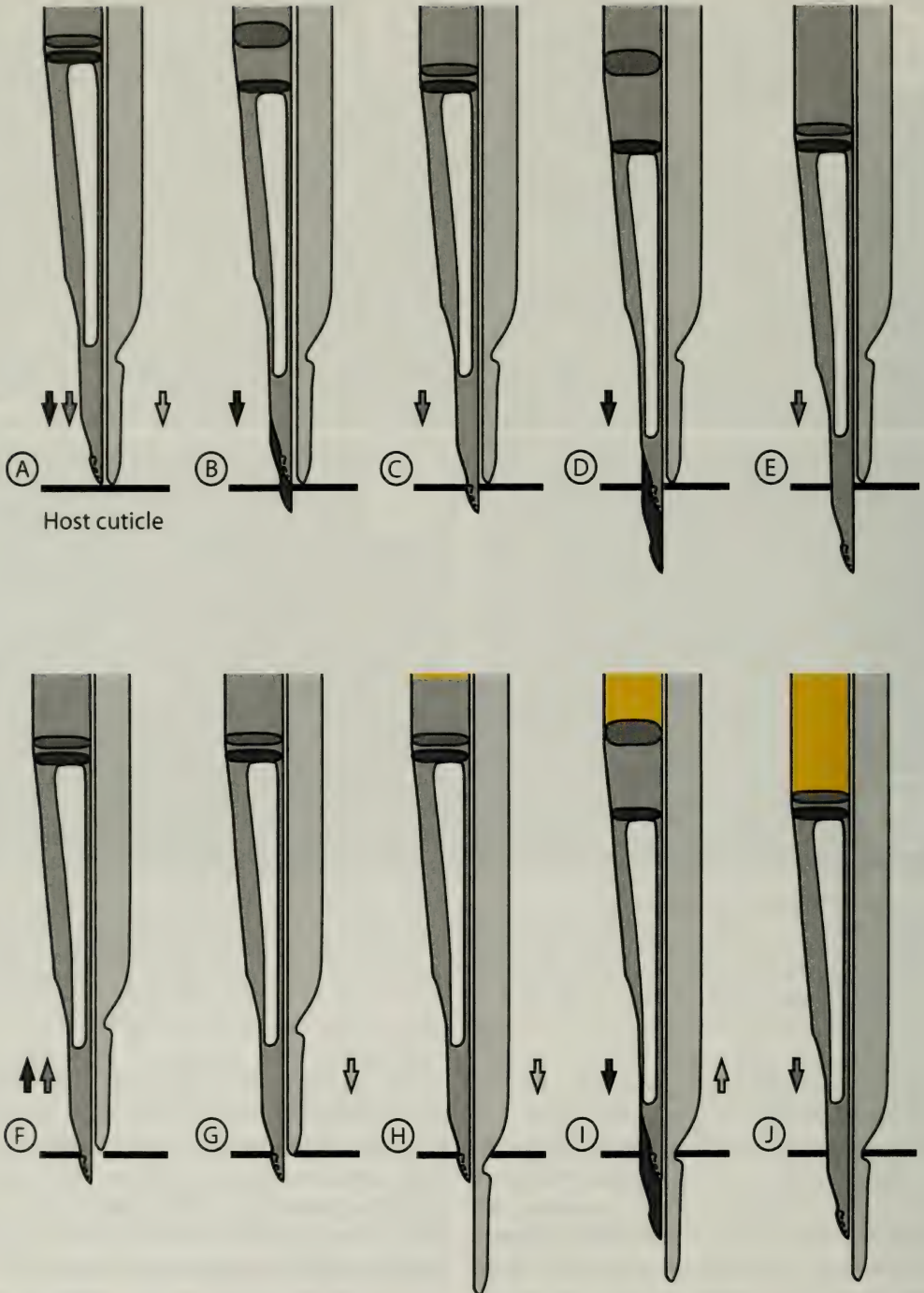


Fig. 8. Illustration of the proposed oviposition sequence in lateral view. A horizontal black line represents the host cuticle. There are two ventral valves, one is light grey and in the foreground, the other is dark grey and in the background. The arrows on the left indicate the movement of the ventral valves; the color of the arrow indicates the movement of the dark grey ventral valve, the light grey ventral valve, or both. An arrow on right indicates movement of the dorsal valve. The valvilli are represented by horizontal ovals, where the dark grey valvillus is attached to the dark grey ventral valve and the light grey valvillus is attached to the light grey ventral



push fluids, and without evidence to the contrary, it is parsimonious to assume the same function for members of Ichneumonoidea. The fluids injected by *H. truncator* are unknown to us, but typically braconid endoparasitoids inject substances that control the immune response of their hosts (Vinson and Iwantsch 1980). Braconid ectoparasitoids usually inject paralyzing venom and have highly muscled venom glands, whereas braconid endoparasitoids only rarely paralyze prey and have relatively weakly muscled, thin walled, venom glands (Edson and Vinson 1979). Though it may be possible that ectoparasitoid braconids pump venom with muscular contractions of the venom gland, the weak musculature of the venom glands of endoparasitoids implies that other mechanisms are employed to deploy venom.

Once the egg is in the loaded position (Fig. 1E), more force would be needed to move the egg due to the bottle-neck formed by the relatively narrow apical section of the ovipositor. We suggest that the valvillus plays the central role in forcing the egg out of the ovipositor and that this is accomplished through hydrostatic pressure. The valvillus by itself is not capable of pushing the egg any further than the position shown in figure 1E. To force the egg completely out of the ovipositor, the lower valve would have to be pushed to a point where the valvillus is aligned with the tip of the dorsal valve. We have never seen an ovipositor in this position and believe it to be impossible in an intact system. We propose that liquid from the venom gland is moved into the egg canal; the valvilli then prevent proximal fluid flow (acting like check valves which allow flow in only one direction).

Distal movement of either ventral valve results in hydrostatic pressure that forces the egg distally. The convex-apical shape of the valvilli also suggests that they act as one-way valves. Any pressure on the apical side of a valvillus will flatten it and create a larger radius of curvature and hence transmit more sealing pressure against the wall of the canal (much like a water dam on a river), whereas any pressure on the proximal side of a valvillus will deform the shape to a smaller radius of curvature and hence result in the loss of seal between the valvillus and the canal wall.

When a ventral valve is pulled back, its valvillus is flush with the wall of the egg canal (Figs 4B, 8G). When a ventral valve is pushed apically, the valvillus blocks the egg canal and pushes against any liquids apical to it (Figs 4D, 8K–L). The hydrostatic force is applied to eggs in the apical or loaded position. This action would create negative pressure in the portion of the egg canal basal to the valvillus, which would cause more fluid, and perhaps the next egg to be drawn into it. A problem with this simple scenario is illustrated in figure 1E, where there appears to be an egg obstructing the base of the egg canal. To circumvent this blockage, which we observed in most specimens, there is a reservoir at the base of each ventral valve (Fig. 5A–D). We propose that when a ventral valve is pulled back and while the opposing valve is being pushed forward and creating negative pressure in the egg canal, the reservoir fills with venom and forms a conduit through which fluids flow into more apical parts of the egg canal (Fig. 8H–T). A preliminary survey found basal reservoirs, similar to those found in *H. truncator*, present in the

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valve. When the valvillus is represented by a thin oval, the valvillus is perpendicular and blocks the egg canal. When the valvillus is represented by a large oval, the valvillus is parallel to, and allows movement through the egg canal. In Fig. 8H, venom enters the egg canal, which is represented by the color yellow. The egg is represented by the white, vertical oval. In Fig. 8O the egg begins to exit the ovipositor from a flap on the ventral valve.



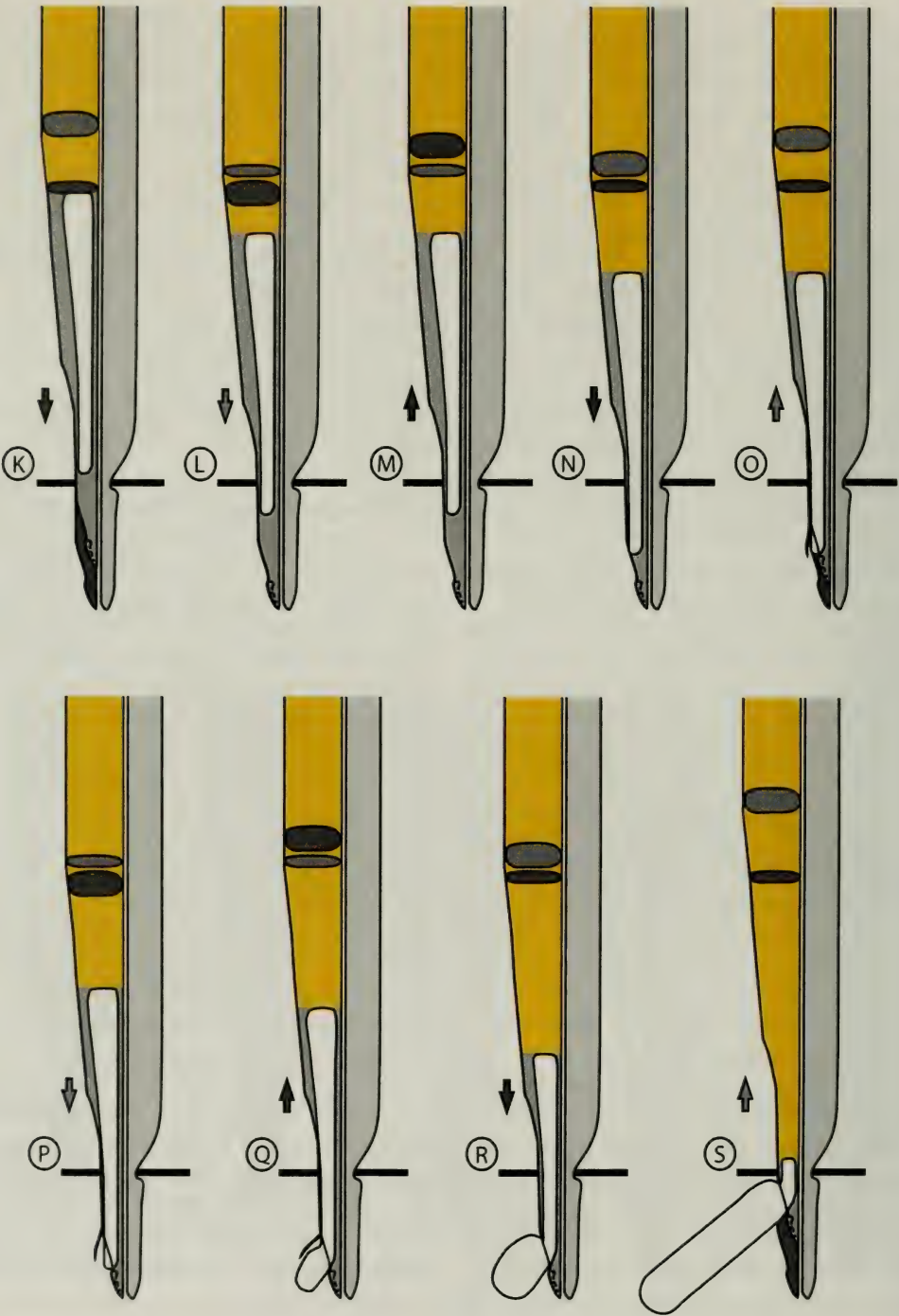


Fig. 8. Continued.



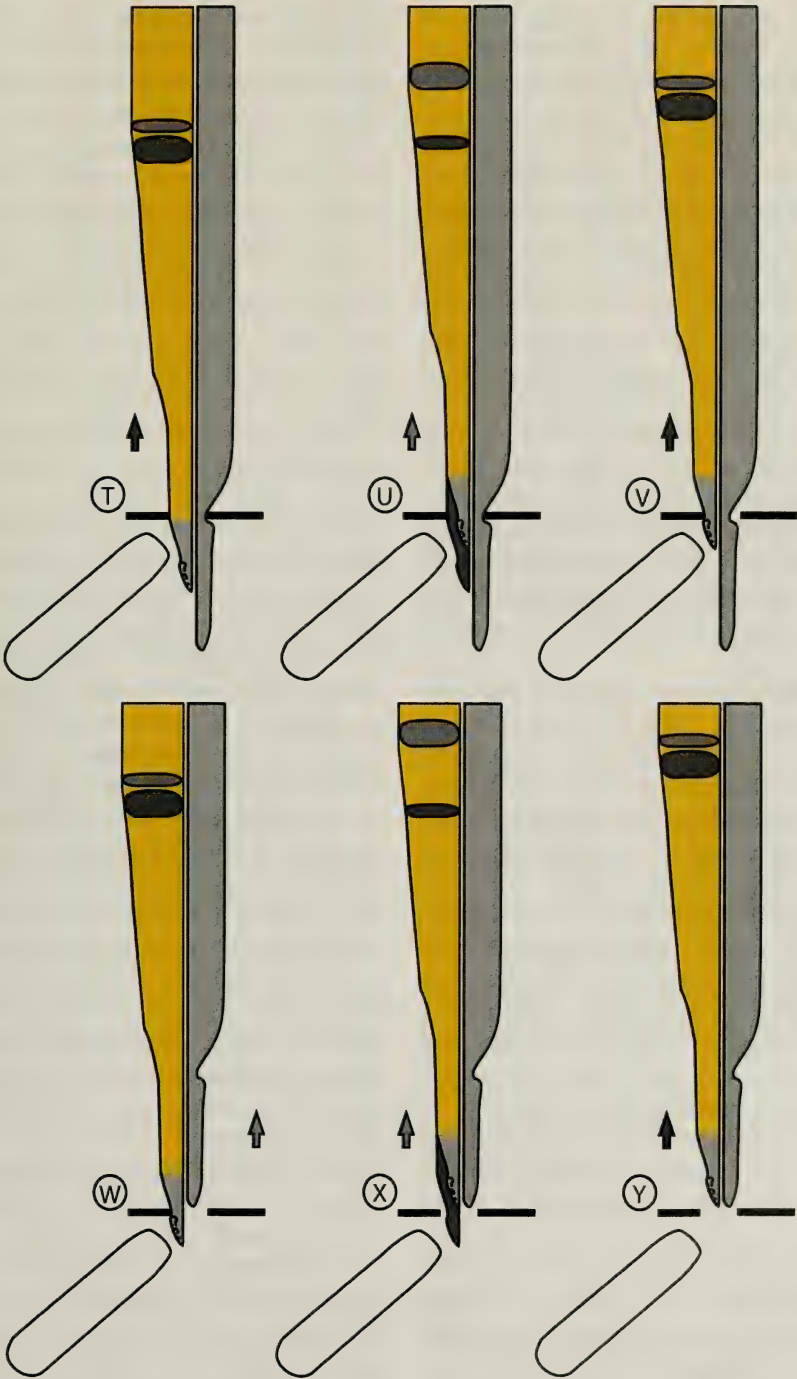


Fig. 8. Continued.



following taxa: Blacinae (Fig. 5E), Helconinae (*Wroughtonia* sp.), Homolobinae, Macrocentrinae (Fig. 5F), Orgilinae, Meteorinae (*Zelex* sp.), and absent in Agathidinae, Braconinae, Doryctinae, Rogadinae, and *Campoletis sonorensis* (Ichneumonidae). This distribution indicates that this feature evolved within the non-cyclostome endoparasitoid lineage of Braconidae. Another possibility that may act in concert with the reservoirs is that fluids run through the medial portion of the egg at the base of the egg canal. Figures 4E, 5C, D illustrate an egg in the basal position and a medial divide is present in the egg that could facilitate the apical displacement of fluids. Congealed fluid is present in the basal area of the egg (Fig. 5C, D). In our dissections, numerous specimens had eggs positioned at the base and all showed the medial division.

The venom gland of *Homolobus truncator* is relatively large (Fig. 2B). The point in time when venom enters the egg canal during oviposition is uncertain. We reason that venom would not be used to push the egg out of the egg canal until after the ovipositor has locked within the host (Fig. 8H). Once the ovipositor has locked into the host cuticle, alternating thrusts of the ventral valves would pull fluid apically, and then be used as a pressurizing medium to push the egg out of the egg canal.

Evidence supporting or consistent with the hypothesis that the valvilli push fluids in the ovipositor of *H. truncator* thereby creating hydrostatic pressure that forces the egg out of the terminal portion of the egg canal are enumerated here. 1) The common ancestor of the Ichneumonoidea and Aculeata undoubtedly laid eggs through the length of the ovipositor and it is clear that the function of the valvilli in the Aculeata is to inject fluids. That the valvilli had the same function in the common ancestor of these two taxa implies that at least in the ground plan of the Ichneumonoidea the valvilli function to

produce fluid pressure. 2) As noted earlier, members of *Itoplectes maculator* do not load their eggs apical to the valvilli (Cole 1981). This indicates that they have a function other than positioning eggs in this species and undoubtedly in many other ichneumonoid taxa. 3) As described in the morphology section, valvilli are set deeply into the wall of the egg canal. This allows them to lay flush against the wall, but it also lends them support when they are functioning to seal the canal (Fig. 2C, D). Figures 4C and 4D show that a single valvillus can completely close the egg canal with the margin of the valvillus supported by the thick wall of the egg canal. The valvilli would have to be strong to produce the hydrostatic pressure necessary to evacuate an egg quickly and the brace formed by the wall of the egg canal could provide the needed support. 4) The valvilli of *H. truncator*, and most other ichneumonoids investigated (Quicke et al. 1992), have a bordering fringe composed of short, thick, setae-like material (Fig. 7A). This would appear to be an effective, flexible seal for the area of the valvillus that contacts the wall of the egg canal. If the role of valvilli were simply to hold eggs in place it is unlikely that such a seal would be necessary. 5) Members of *Wroughtonia* sp. and many other ichneumonoids have multiple valvilli on each ventral valve (Fig. 6F). The spaces between these valves are not sufficient to enclose an egg and therefore all but the most apical valvilli must have a function other than holding an egg in place. 6) To be effectively pushed out of the egg canal with hydrostatic pressure, the basal surface of the egg of *H. truncator* must completely seal the egg canal. Any fluid escaping to the lateral surface of the egg would be counterproductive, not only because it would be a waste of venom, but also because it would press the lateral surface of the egg against the wall of the egg canal thereby increasing frictional forces and making it more difficult to move the egg. Figures 5B and 5C show



such a seal on the apical end of the egg of *H. truncator*. It is not clear if there are special structures on this end of the egg or if it is simply plastic enough to take the form of the egg canal. 7) The apical portion of the inner wall of the ventral valve of *H. truncator* is mostly smooth (Fig. 2E); the ctenidia that are present are long, flexible and restricted to the edges of the valves. Clearly they cannot function to push eggs in this area.

Evidence presented earlier showed that ctenidia are capable of moving eggs through the basal portion of the egg canal, so the question of why there is another mechanism acting at the apex is an important one to address. We suggest that the primary reason, in *H. truncator*, is to facilitate rapid expulsion of the egg. Even at the base of the ovipositor the surface of the egg is scarred by the forces applied by the ctenidia (Fig. 4E, F). The surface of the egg of *H. truncator* is soft and pliable as indicated by its distortion as it passes through the egg canal (Fig. 5C, D) and the ctenidial scars (Fig. 4F). Adult females of *H. truncator* attack active exposed Lepidoptera larvae and the shorter the period of contact with them the less likely it would be that the host would be able to escape or inflict damage. There are no published observations of the oviposition speed for *H. truncator* known to us. However the ovipositor of the ichneumonid endoparasitoid *Venturia canescens* is similar in that it has a pre-apical notch on the dorsal valve. Rogers (1972) reported observing that oviposition in *V. canescens* takes a "fraction of a second". We speculate that if ctenidia were employed to force an egg quickly out of the egg canal that the ctenidia and/or the surface of the egg would be subject to tearing. Near the apex of the egg canal, the egg is tightly packed into a small space that becomes increasingly narrow. The force needed to move an egg is greater here than it would be at the base of the egg canal. The need for a quick delivery of the egg and the greater frictional forces in the apical part of

the egg explain the advantages of using hydrostatic pressure.

*Phase 4: Egg laying and ovipositor withdrawal.*—There is a longitudinal ridge, the sperone, on the inner surface of the dorsal valve (Fig. 3A, C, D) (Zinna 1960; Rahman et al. 1998) and we propose that it plays a role in egg evacuation. The sperone was first described by Zinna (1960) for a similar structure found in some chalcidoids and its distribution within the Braconidae was enumerated by Rahman et al. (1998). To date no function has been proposed for the sperone and it is possible that this varies among taxa. For members of *H. truncator* we suggest that it functions as a substrate that forces the egg to exit from flaps situated near the apex of the ventral valves (Fig. 2C). The sperone begins as a shallow ridge basal to the pre-apical notch and gradually increases in height as it approaches the apex of the dorsal valve to the point that it occupies most of the lumen of the egg canal. Figure 3A shows the apex of the dorsal valve in lateral view; the ventral surface of the sperone is visibly bulging out such that, if the ventral valve were not retracted, the sperone would occupy most of the dorsal side of the egg canal as well. Figures 1D and 2C show that the part of the sperone that is most produced is situated directly opposite the flaps of the ventral valves. We suggest the following scenario for the final egg laying stage in *H. truncator*. When the apex of the egg hits the sperone it is pushed toward the ventral surface of the egg canal and when it reaches the ventral flaps it is pushed out through the flaps (Figs 2C, D, 8O–Q). A reviewer of the first draft of this paper suggested that the flaps could function as a seal to contain venom. After examining additional specimens, we found one instance of the egg partially exiting the ovipositor from the ventral valve flaps (Fig. 2C, D). Furthermore, if the sole function of the flaps were to seal venom, one would expect them to be present in aculeate taxa. We examined specimens of

Scoliidae, Chrysidae, Rhopalosomatidae, Vespidae, Sphecidae, Halictidae, and Megachilidae under a scanning electron microscope and none possesses flaps at, or near, the apex of the ventral valves. Furthermore, since the eggs of *H. truncator* are loaded at the tip of the ovipositor they effectively block any fluids from escaping. Finally, the flaps are relatively thin and flexible and they lack muscle; it seems that little pressure need be exerted on them to cause them to open. In the closed position the flaps would provide a weak seal that would prevent evaporation of the little fluid remaining on the surface of the egg canal while the next egg moves into the loaded position.

The eggs are elongated when they are compressed in the egg canal (drawn to scale in Fig. 8A–P) and it would undoubtedly require multiple alternating thrusts of the ventral valves to effectively evacuate the entire egg. Since fluids fill the contents of the egg canal between the valvelli and the base of the egg, these too would flow out of the flaps following oviposition.

As the egg emerges from the ovipositor, elastic strain energy stored in the chorion provides additional force to assist egg evacuation from the ovipositor (Fig. 8Q–T). Assuming that the chorion does not undergo any molecular restructuring during oviposition and that it has not undergone appreciable plastic deformation throughout its volume, we can assume that it is purely elastic. As such, the initial energy required to deform the egg, to allow passage through the egg canal, will be returned in full. The relaxed shape of the eggs has a larger degree of sphericity (lower surface area) than does the deformed shape in the canal, thus the amount of elastic strain energy stored in the chorion is proportional to the change in the sphericity (i.e., change in surface area). In the egg canal the egg is constrained in an exaggerated elongated shape (metastable state) and upon emergence from the canal the constraint is removed and the relaxed

shape of the egg is attained, which is more stable and more spherical. The stored elastic strain energy is returned when the egg exits the canal to attain its stress free shape; the elastic strain energy is a strong driving force for egg extraction. As the egg first emerges from the flaps in the lower valves the egg expands in the radial direction, and contracts in the axial direction (Fig. 8Q–T). The shape change, in particular the axial contraction, assists egg extraction. Upon emergence the egg's diameter increases, so the contractile force of the chorion returning to its original stress-free state pulls the remainder of the egg out of the canal, much like a siphon. Undoubtedly a suction force occurs within the egg canal which could draw other eggs or fluid apically in the canal. A video demonstration of this phenomenon can be seen in the oviposition of *Rhyssella curvipes* (Gravenhorst) and *Pseudorhyssa alpestris* (Holmgren) (Skinner and Thompson 1960). Fig. 8Q–Y depicts an approximation of the size and shape of an egg exiting the egg canal, as the exact dimensions of the egg upon exiting the ovipositor is unknown. The apical narrowing of the egg canal also reveals that a larger back pressure will exist just before the apical end of the egg reaches the flaps, preventing the egg from slipping out unnecessarily; more energy will be required to deform the egg through the smaller opening, hence the egg would tend to relax by moving distally. The valvelli play an important role here to prevent back flow, as does the higher number, density, and distribution of ctenidia at the apical end of the ventral valves and flaps (Fig. 2E).

Withdrawal of the ovipositor from the host would necessarily begin with the ventral valves (Fig. 8S). Once the apices of the ventral valves are recessed to a point where they are near the notch of the dorsal valve (Fig. 8S–V), the surface of the ovipositor would no longer be pressed against the host cuticle and the entire ovipositor could be withdrawn without resistance



(Fig. 8W–Y). The shallow angle of the pre-apical notch facilitates easy extraction; it permits only a small axial force in opposition to withdrawal and actually helps to disengage the dorsal valve from the host cuticle as compared to a recurved barb which would hold fast (Fig. 1B).

Summary

We wish to reiterate the point that we are proposing hypotheses not facts. It is our hope that the ideas presented here will stimulate future research that will hopefully result in corroboration, but perhaps refutation, of our hypotheses. Of greatest interest to us is the function of the valvilli. They show great variability in form, location, and number throughout the Ichneumonoidea, and an understanding of their functional morphology could provide many insights into life history traits. Furthermore, the taxonomic distribution of the reservoirs at the bases of the ventral valves, the presence of apical flaps, and undoubtedly many other ovipositor characters could provide useful information for phylogenetic studies of the ichneumonoidea.

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## A Revision of *Bephrata* and *Isosomodes* (Hymenoptera: Eurytomidae)

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**Abstract.**—The genera *Bephrata* Cameron and *Isosomodes* Ashmead are redefined and redescribed. Twenty-two species are described as new: *B. atra*, *B. bouceki*, *B. camacho*, *B. chica*, *B. christeri*, *B. citri*, *B. clava*, *B. flava*, *B. leptogaster*, *B. lorraineae*, *B. nigracephala*, *B. noyesi*, *B. nublada*, *B. petiolata*, *B. stichogaster*, *B. ticos*, *I. azofiefai*, *I. landoni*, *I. paradoxus*, *I. parkeri*, *I. colombia*, and *I. similis*. Previous nominal species are redescribed: *B. bahiae* (Ashmead), *B. cultriformis* (Ashmead), *B. ruficollis* Cameron, *I. gigantea* (Ashmead), and *I. nigriceps* Ashmead. One new synonymy is proposed: *I. brasiliensis* Ashmead 1904 with *I. gigantea* (Ashmead 1886), **n. syn.** Keys are provided for separating the species in each genus. Available evidence suggests that the species in these two genera are egg parasitoids of Tettigoniidae (Orthoptera).

**Key words.**—*Bephrata*, *Isosomodes*, Eurytomidae, egg parasitoids, Tettigoniidae, orchids

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In their phylogenetic analysis of the Eurytominae (Eurytomidae), Lotfalizadeh et al. (2007) recognized the *Bephrata* genus group as one of the basal clades in the subfamily. Among the more readily observable characteristics they cited for characterizing this group are elongate body with a flattened scutellum, subcircular head (in frontal view) with short malar space and torus situated well above lower eye margin, stigmal vein almost as long as, to slightly longer than, marginal vein and forming an acute angle (40° or less) with the postmarginal vein, and the postmarginal vein is nearly always longer than the marginal vein.

The *Bephrata* genus group includes *Bephrata* Cameron and *Isosomodes* Ashmead, both of which are known principally from the New World. Lotfalizadeh et al. (2007: 470) synonymized *Aximogastra* Ashmead with *Bephrata*. Carefully examining their appendix 2 (p. 508), “*Bephrata* Cameron 1884” is neither in bold type nor set off from the preceding treatment of *Aximopsis* and its synonyms. Upon rapid scanning of

the appendix, it might appear that *Aximogastra* was synonymized erroneously with *Aximopsis* Ashmead when this is not the case. In any event, the type species of *Aximogastra* (*A. bahiae* Ashmead) is explicitly combined with *Bephrata* on page 509 (Lotfalizadeh et al. 2007), implicitly synonymizing the two genera.

The three nominal species of *Bephrata* described from southern Asia (*B. dalhousiensis* Mukerjee, *B. kumaomensis* Mukerjee, *B. nepalensis* Mukerjee (Mukerjee 1981)) do not appear congeneric with the type species (*B. ruficollis* Cameron) from the Neotropics based on the written descriptions and illustrations, but we have not examined those species. Lotfalizadeh et al. (2007) mention an undescribed species of *Bephrata* (cited as *Aximogastra*) from Guinea, and thus this genus apparently is present in the Old World. Although the biologies of *Bephrata* and *Isosomodes* are poorly known, the available evidence indicates that they are parasitoids of eggs of Tettigoniidae (Orthoptera), specifically *Buocrates capitatus* (De Santis 1989) plus

Table 1. Morphological differences between *Bephrata* and *Isosomodes*.

	<i>Bephrata</i>	<i>Isosomodes</i>
Sculpture of lower face	With radiating striae	Without radiating striae
Intertricular space*	Less than torular diameter; compressed above into laminate projection	Greater than torular diameter; angulate above
Last two flagellomeres of female	Separated, never wider than preceding flagellomeres	Appressed, sometimes slightly wider than preceding flagellomeres
Apex of male scape	With light colored oval area; absent in <i>B. leptogaster</i>	Without light colored oval area
Posterior genal margin*	Usually carinate; ecarinate in <i>B. clava</i> and <i>B. cultriformis</i>	Ecarinate
Subforaminal plate on postgenal bridge*	Discoid plate absent	Discoid plate present, but not well delimited medially
Notauli and axillular grooves*	Evident to mostly obliterated	Obliterated
Angle between dorsal surface of scutellum and propodeum	Variable, but often less than 135 degrees	Greater than 135 degrees
Procoxa*	With oblique groove at base of anterior surface; absent in <i>B. clava</i> and <i>B. cultriformis</i>	Without oblique groove on anterior surface
Marginal vein*	> stigmal vein	< stigmal vein
Hypopygium*	Usually extending beyond middle of gaster	Not reaching middle of gaster
Number of pairs of setae at apex of hypopygium	5–18, except in <i>B. citri</i>	2–4 pairs

\* = characters listed by Lotfalizadeh et al. 2007

*Bucrates* sp. and *Tettigonia* sp. (Herting 1973). A sample of tettigoniid (Pseudophyllinae) eggs obtained by PH yielded a rearing record for *B. citri*, **n. sp.**

Lotfalizadeh et al. (2007) listed six apomorphies for *Bephrata* (and *Aximogastrea*) and three for *Isosomodes*. These are given in Table 1, together with some additional characters for distinguishing the two genera. Because most of the tabulated differences include a few exceptions, we have used a combination of characters to characterize these two genera. In the New World, *Bephrata* includes three nominal species: *B. ruficollis* Cameron, *B. cultriformis* Ashmead, and *B. bahiae* (Ashmead). *Isosomodes* also included three nominal species: *I. gigantea* (Ashmead), *I. brasiliensis* Ashmead, and *I. nigriceps* Ashmead. Here we describe 16 new species of *Bephrata*, six new species of *Isosomodes*, and propose one new synonymy (*I. brasiliensis* with *I. gigantea*), thus bringing the total number of species in the New World to 19 and 8, respectively.

MATERIALS AND METHODS

Descriptions of species are based on the female holotypes. Two species were originally described based on males: *I. gigantea* and *I. nigriceps*. Structures not visible on the holo- or lectotype but shown in the figures are indicated by brackets [ ].

*Specimen examination and preparation:* Specimens in ethanol were dehydrated through increasing concentrations of ethanol to HMDS (Heraty and Hawks 1998) before point or card mounting. Images of specimens were produced by scanning electron microscopy (SEM) and an EntoVision Imaging Suite. A Nikon SMZ1500 stereomicroscope with 10× oculars (Nikon C-W10X/22) and a Chiu Technical Corp. Lumina 1 FO-150 fiber optic light source was used for card- and point-mounted specimen observation. Mylar film was placed over the ends of the light source to reduce glare. Scanning electron microscope (SEM) images were taken with an Amray 1810 (LaB<sub>6</sub> source). Some specimens were cleaned of external debris with bleach and



distilled water following Bolte (1996) and affixed to 12.7× 3.2 mm Leica/Cambridge aluminum SEM stubs with carbon adhesive tabs (Electron Microscopy Sciences, #77825-12). Stub-mounted specimens were sputter coated using a Cressington Scientific 108 Auto with a gold-palladium mixture from at least three different angles to ensure complete coverage (~20–30 nm coating). Color images were obtained using an EntoVision Imaging Suite, which includes a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. This system fed image data to a desktop computer where Cartograph 5.6.0 (Microvision Instruments, France) was used to capture a fixed number of focal planes (based on magnification); the resulting focal planes were merged into a single, in-focus composite image. Uniform lighting was achieved using a LED illumination dome with all four quadrants set to 99.6% intensity. Terminology generally follows that of Gibson et al. (1997), except for a few terms from Lotfalizadeh et al. (2007), such as intertorular space (instead of interantennal space), adscrobal carina (anterior border of femoral depression), epicnemium (instead of mesepisternum), and characters on the posterior surface of the head. These latter characters were not examined for all species and are reported in the generic descriptions based upon the taxa for which they were observed (*B. ruficollis*, *I. azofiefai*, *I. similis*). Specimen with data labels similar to "COSTA RICA INBioCRI000645008" (numeric suffix differs) have been barcoded by INBio. Terminology for surface sculpture (e.g. nitid = shiny) follows that of Harris (1979). Abbreviations for collections are BMNH (The Natural History Museum, London), CNC (Canadian National Collection, Ottawa), INBio (Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica), IAVH (Instituto Alexander von Humboldt, Bogotá, Colombia), MZCR (Museo de Zoología, Universidad de Costa Rica), and

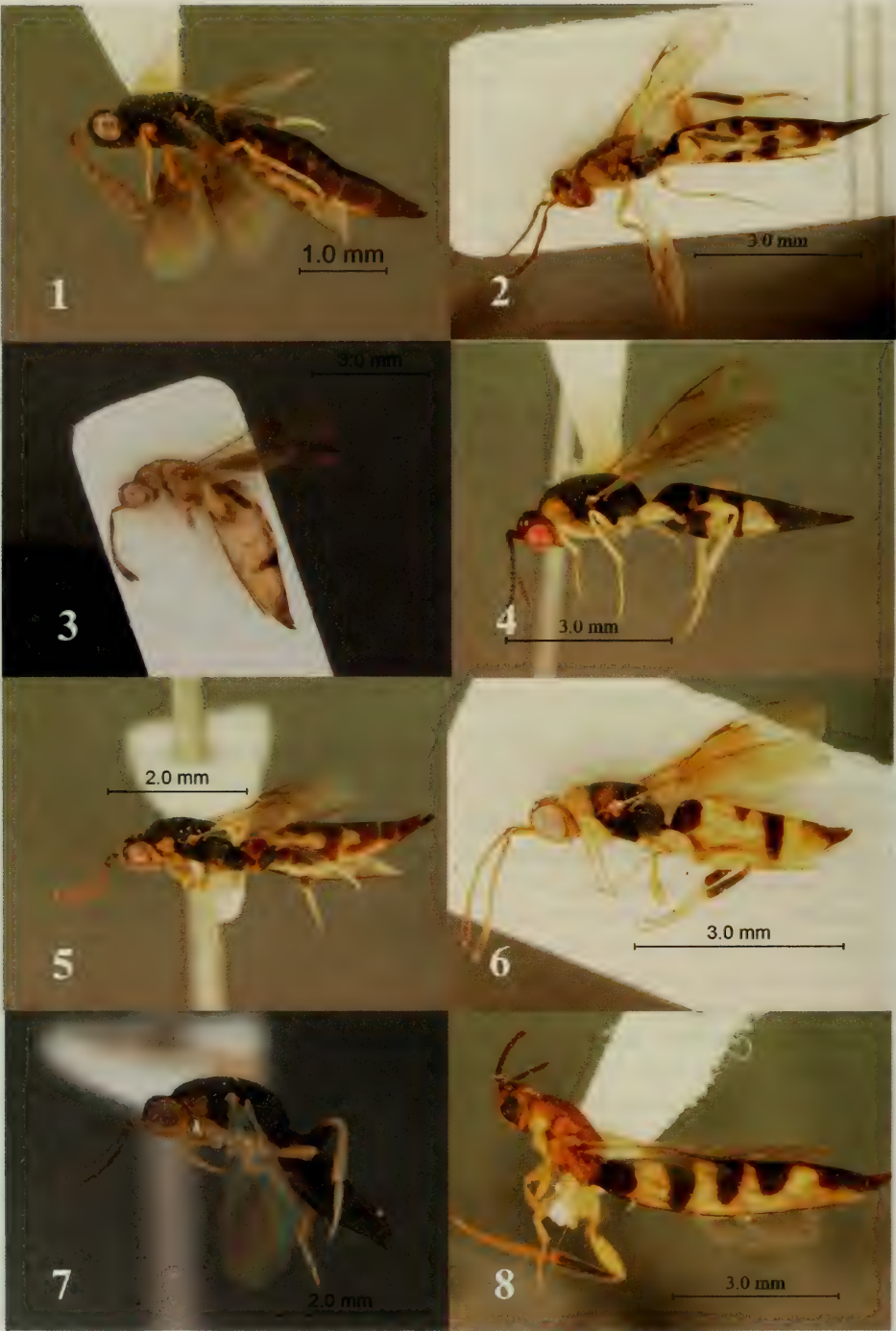
USNM (National Museum of Natural History, Washington, D.C.). Materials from Ecuador are held on indefinite loan from Escuela Politécnica Nacional, Quito, Ecuador (EPNC). In 1999, Napo province in Ecuador was subdivided by the creation of Orellana province from the eastern ¼ of the former Napo province. Label data reported herein reflect Napo province as previously defined, given dates of collection. Lectotypes established herein, in accordance with Article 74.7.3 (ICZN 1999), are designated in order to ensure nomenclatural stability.

### *Bephrata* Cameron

*Bephrata* Cameron 1884:109. Type species: *Bephrata ruficollis* Cameron, by monotypy.

*Aximogastra* Ashmead 1904: 261. Type species: *Aximogastra bahiae* Ashmead, by monotypy. Synonymy by Lotfalizadeh et al. 2007: 508.

*Description (females).*—Length 3.2–8.3 mm. Color: Usually a combination of yellow (or orange/reddish yellow) and black, mostly black in *B. atra*, *B. chica*, *B. citri*, and *B. nigracephala*; middle terga of gaster often with black band along posterior margin (appearing like vertical tiger stripes), becoming weaker ventrally (Figs. 1–19). *Sculpture*: Head (except gena), dorsal mesosoma, lateral and posterior part of epicnemium, metapleuron, and lateral areas of propodeum covered with setigerous foveae ('umbilicate punctures'), interstices appearing microreticulate at low magnification (Fig. 28); supraclypeal area with striae converging on clypeus (Fig. 29), gena and lateral panel of pronotum weakly sculptured, coriarius-substrigulate; prepectus weakly sculptured, shallowly concave along dorsoventral axis; femoral depression coriarius and/or substrigulate, mesepimeron less sculptured (Fig. 30); metepimeron and lateral areas of propodeum more strongly sculptured (deeply foveate to alveolate) than rest of body; coxae weakly sculptured, outer surface of metacoxa coriarius; metatibia

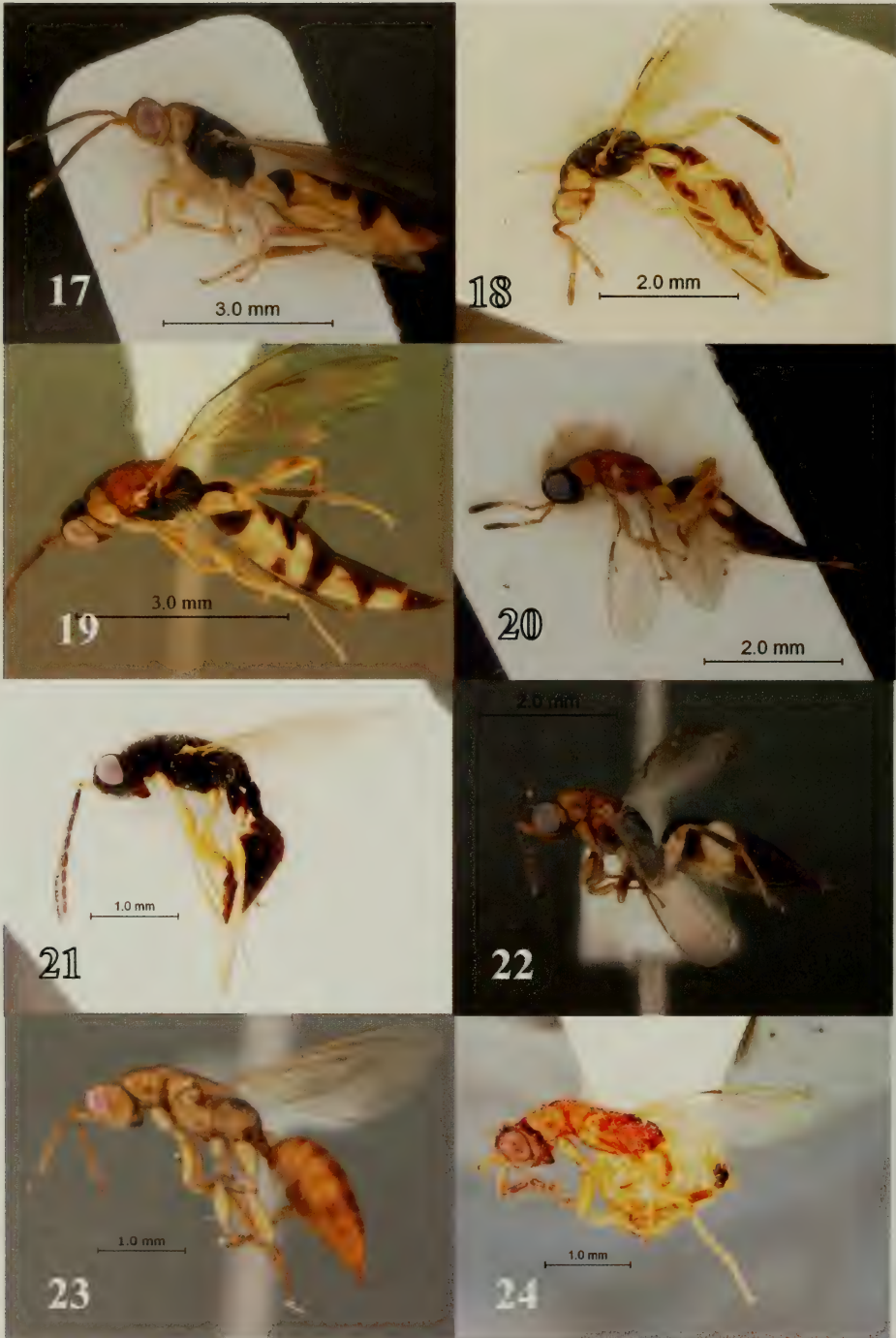


Figs 1–8. 1, *Bephrata atra*, habitus; 2, *B. bahiae*, habitus; 3, *B. bouceki*, habitus; 4, *B. camacho*, habitus; 5, *B. chica*, habitus; 6, *B. christeri*, habitus; 7, *B. citri*, habitus; 8, *B. clava*, habitus.



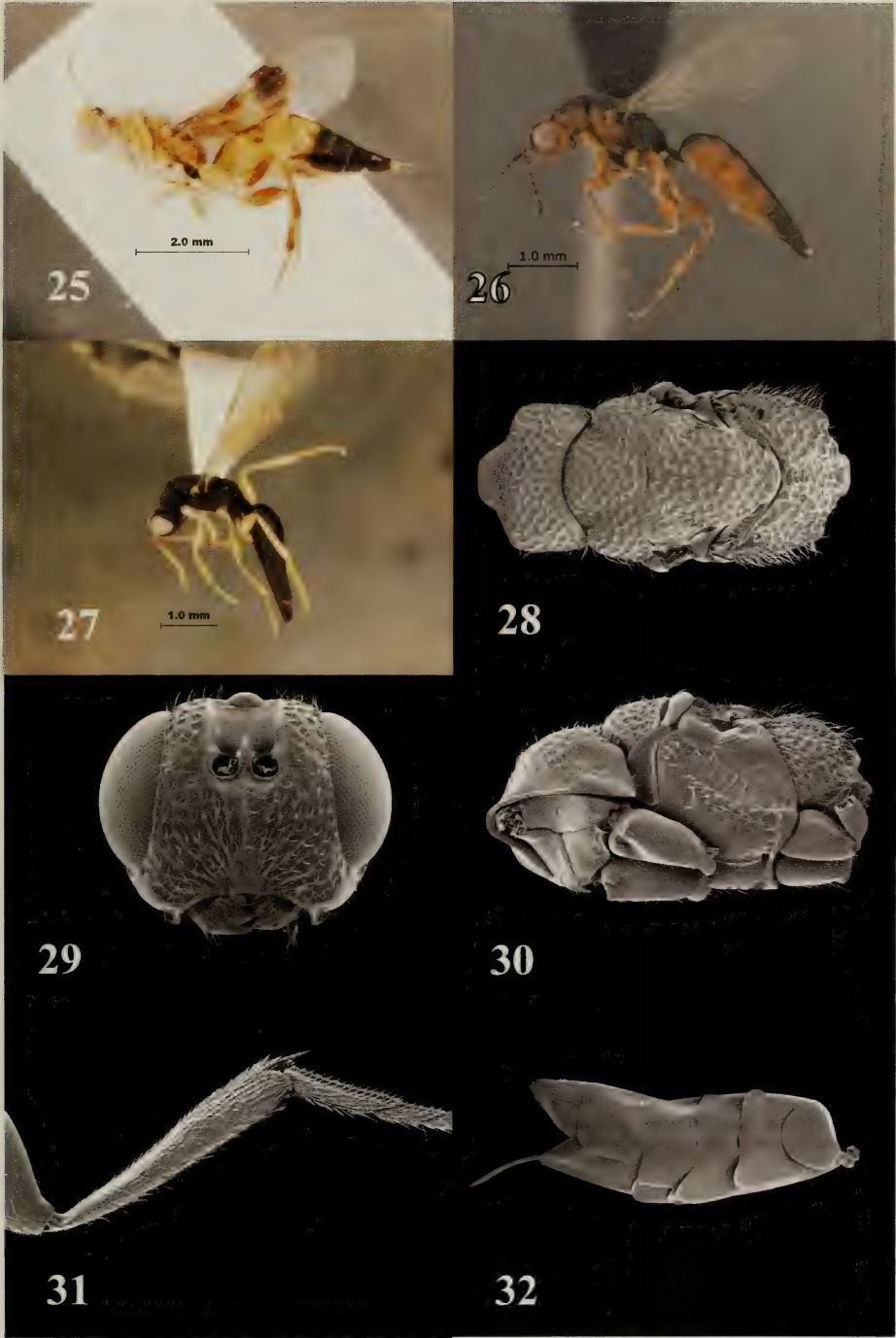


Figs 9–16. 9, *Bephrata cultriformis*, habitus; 10, *B. flava*, habitus; 11, *B. leptogaster*, habitus; 12, *B. lorraineae*, habitus; 13, *B. nigracephala*, habitus; 14, *B. noyesi*, habitus; 15, *B. nublada*, habitus; 16, *B. petiolata*, habitus.

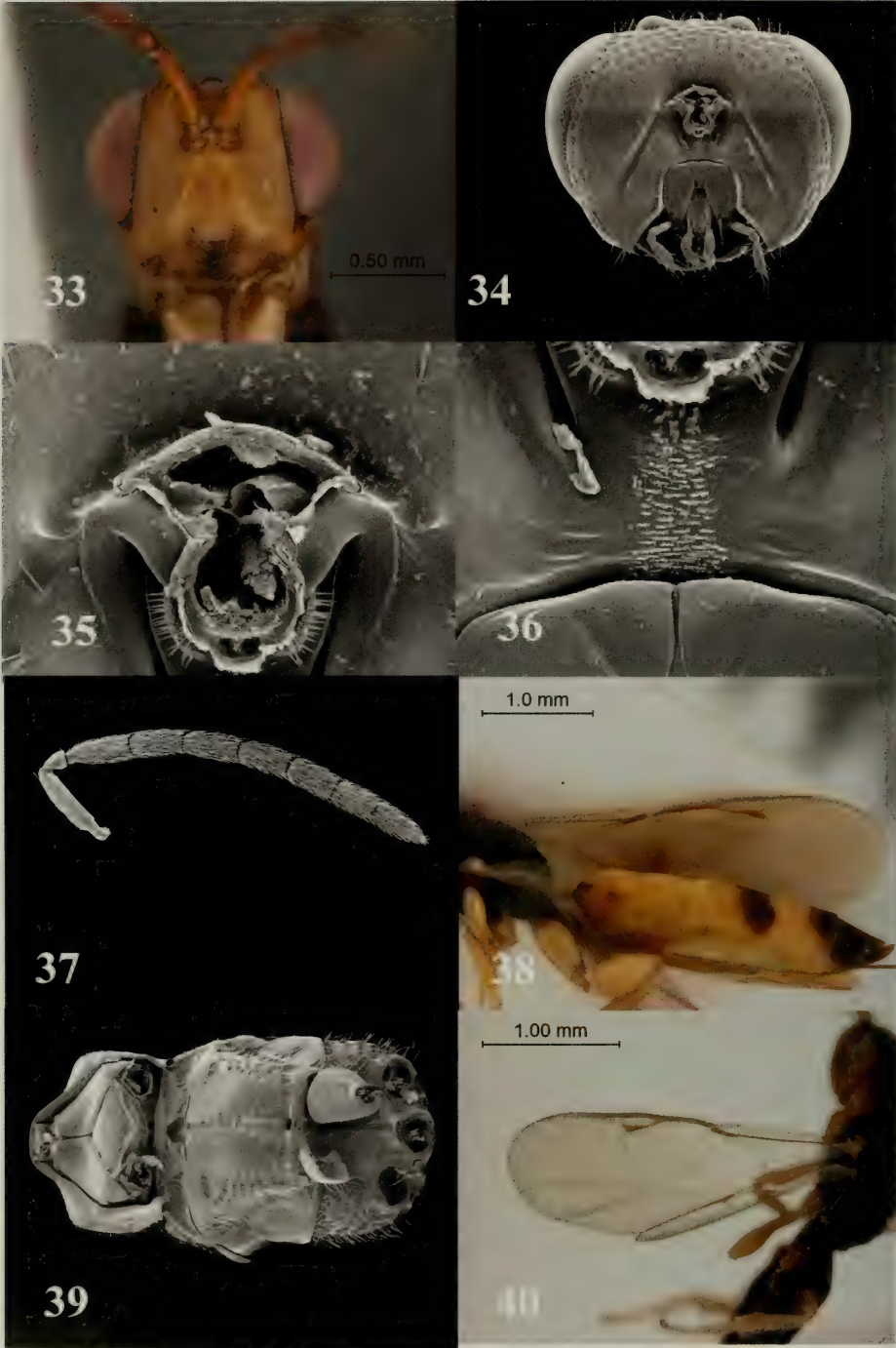


Figs 17–24. 17, *Bephrata ruficollis*, habitus; 18, *B. stichogaster*, habitus; 19, *B. ticos*, habitus; 20, *I. azofiefai*, habitus; 21, *I. gigantea*, habitus; 22, *I. colombia*, habitus; 23, *I. landoni* habitus; 24, *I. nigriceps*, habitus.





Figs 25–32. 25, *Isosmodes paradoxus*, habitus; 26, *I. parkeri*, habitus; 27, *I. similis*, habitus; 28, *B. ruficollis*, dorsal mesosoma; 29, *B. ruficollis*, anterior head; 30, *B. ruficollis*, lateroventral mesosoma; 31, *B. camacho*, metatibia; 32, *B. ruficollis*, lateral gaster.



Figs 33–40. 33, *Bephrata ruficollis*, anterior head; 34, *B. ruficollis*, posterior head; 35, *B. ruficollis*, foramen magnum; 36, *B. ruficollis*, postgenal bridge; 37, *B. ruficollis*, female antenna; 38, *B. ruficollis*, fore wing and gaster; 39, *B. ruficollis*, ventral mesosoma; 40, *B. citri*, fore wing.





Figs 41–48. 41, *Bephrata camacho*, lateral gaster; 42, *B. noyesi*, male antenna; 43, *B. lorraineae*, male scape; 44, *B. leptogaster*, male antenna; 45, *B. azofiefai*, male antenna; 46, *B. ruficollis*, male antenna; 47, *B. cultriformis*, no genal carina; 48, *B. cultriformis*, procoxae.

appearing longitudinally rugose from presence of raised, elongate carinae (Fig. 31); metasoma nitid, often finely imbricate posteriorly (Fig. 32). Head: Slightly wider than high in frontal view; mandible with two pointed teeth ventrally and a truncate tooth dorsally; anterior clypeal margin straight (Fig. 29); torus situated above middle of eye and antennal scape often extending above vertex; intertorular space narrow, with a semicircular plate (in lateral view; Fig. 33) extending to base of scape, continuing as raised lineation in middle of scrobal basin but becoming very weak and often difficult to discern dorsally; scrobal basin very weakly sculptured, carinate laterally; anterior ocellus situated adjacent to scrobal basin, usually separated by a transverse lineation; malar sulcus weak, usually only evident at ventral and dorsal end; gena convex, genal carina usually present, at least ventrally (absent in two species; see Comments). Antennal scape relatively short, not much longer than first funicular segment, anellus very small, funicular segments much longer than wide; clava with 3 fused segments; first funicular segment slightly tapered at base; funicular segments and clava with 2–4 irregular, overlapping rows of longitudinal sensilla (MPS), covered with subdecumbent setae, about  $0.8\times$  width of corresponding segment; apex of clava with fine 'crown' of microsetae (Fig. 37). Posterior surface of head with lateral foraminal plates distinct dorsally and laterally and extend to mid length of postgenal bridge sulci; postgenal bridge sulci deep and complete, bridge ornamented with digitiform cuticular expansions, postgenal present, straight, indistinct dorsally, postgenal lamina absent (Figs. 34–36). Mesosoma: About twice as long as wide (length  $1.8\text{--}2.3\times$  width), dorsal surface straight in lateral view, scutellum flat (Fig. 38), propodeum usually sloping steeply ventrally; notauli variable but not deep; axillular groove often obliterated, sometimes evident as row of foveae or weak line; lateral

surface of prepectus triangular, narrow posteriorly, with posterior corner rounded; subventral carina of prepectus visible in lateral view; epicnemium in lateral view broad and evenly curved, without a differentiated mesopleural shelf (simple transverse carina in front of mesocoxae; Fig. 39); femoral depression of mesopleuron shallowly concave, usually demarcated anteriorly by adscrobal carina (rarely absent). Procoxa usually convex anteriorly, laminate anteroapically, basal anterior surface usually with a broad, oblique, channel-like depression (for reception of lower head), bordered mesally by a carina (Fig. 30) (depression and carina absent in two species; see Comments); metafemur about  $3\times$  as long as wide; metatibia with two apical spurs, the shorter spur usually pointed (like the longer spur), but blunt in two species (see Comments). Fore wing with postmarginal vein longer than marginal vein, stigmal vein slightly shorter than marginal vein, speculum and basal cell setose (like rest of wing) (Figs. 38, 40). Metasoma: Petiole asetose, usually wider than long (quadrate in *B. noyesi*; elongate in *B. nigracephala* and *B. petiolata*); gaster elongate (length  $2.2\text{--}6.9\times$  height), weakly sclerotized, [collapsing and strongly compressed laterally in dried specimens]; gastral terga 1–5 usually somewhat similar in length; hypopygium nearly always reaching beyond midlength of gaster, often nearly to apex, ventral line with 5–18 pairs of setae (Figs. 32, 41); ovipositor sheaths tilted upward at apex, terminating behind Gt7.

Males.—Presently unknown in four of nineteen species: *B. atra*, *B. citri*, *B. nigracephala*, and *B. petiolata*. Usually slightly smaller, darker (especially the gaster) than female. Antennal scape with small, light-colored oval area at apex (opposite insertion of pedicel), which may or may not be situated on a knoblike projection (Figs. 42, 43) (depending on species), but oval area absent in *B. leptogaster* (Fig. 44); flagellomeres narrowed at each end, with elongate setae at least  $2\text{--}3\times$  width of flagellomere



(Fig. 45), except in *B. ruficollis*, which has shorter and more dense setae (Fig. 46).

*Comments.*—*Bephrata clava* and *B. cultriformis* lack the genal carina and procoxal depression (the two characters probably being functionally related; Figs. 47, 48), as in *Isosomodes*. These two species have the metatibia with the short apical spur blunt (instead of pointed; Fig. 49), unlike any other species of *Bephrata* or *Isosomodes*, except males of *B. leptogaster*, which are anomalous in other characters (the antennal scape and sculpturing of the mesosoma). In all other characters examined *B. clava* and *B. cultriformis* resemble other *Bephrata*. The number of setae on the apex of the hypopygium is a fairly reliable and previously unreported means of separating *Bephrata* (5 or more pairs of setae) from *Isosomodes* (3–4 pairs); the only exception is *B. citri*, which appears to have only three pairs of setae, although this is based on one specimen (the only specimen with an exposed hypopygium).

*Biology.*—The specimens examined were collected by Malaise trap, hand net, canopy fogging and, less commonly, yellow pan traps; none were collected at lights. The

only host record is for *B. citri*, which emerged from eggs of Pseudophyllinae (Orthoptera: Tettigoniidae) inserted into a citrus branch (Fig. 50). *Bephrata chica*, *B. leptogaster*, *B. lorraineae*, and *B. stichogaster* included specimens that were intercepted at ports-of-entry into the United States in association with orchids (*Cattleya*, *Laelia*), suggesting that they emerged from host eggs (possibly tettigoniid) in these plants. An intercepted specimen of *B. camacho* was reared from a palm (*Chamaedorea*) stem; one specimen of *B. stichogaster* was associated with *Philodendron* (Araceae) stems and one *B. chica* with bromeliads. With respect to phenology, the available information suggests that species of *Bephrata* show little seasonality with respect to adult activity. Two of the most common species in Costa Rica, *B. camacho* and *B. ruficollis*, have been collected every month of the year.

*Distribution.*—In the New World, species of *Bephrata* have been collected from Mexico (Vera Cruz) to Brazil (Amazonas, Bahia). They occur primarily in the lowlands with some species occurring at mid-altitudes (up to 1500 m); in Costa Rica no specimens have been collected above 1600 m.

KEY TO SPECIES OF BEPHRATA

- 1      Procoxa without sinuous groove on anterior surface (Fig. 48); metatibia with shorter apical spur peglike (Fig. 49) and metatarsus with first tarsomere about as long as combined length of remaining tarsomeres. . . . . 2
- Procoxa with sinuous groove on anterior surface (Fig. 30); metatibia with shorter apical pointed spur (similar to longer spur) and metatarsus with first tarsomere usually longer than combined length of remaining tarsomeres (Fig. 31). . . . . 3
- 2(1)   Mesosoma almost entirely reddish orange (Fig. 8) [Costa Rica] . . . . . *clava*
- Mesosoma predominantly black, except for lateral portion of pronotum, lateral lobes of mesoscutum and axillae (Fig. 9) [Central & Northern South America] . . . *cultriformis*
- 3(1)   Metatibia completely yellow. . . . . 4
- Metatibia black, at least in part. . . . . 6
- 4(3)   Metafemur entirely yellow (Fig. 17); tarsal claws robust; female with last flagellomere of antenna white, hypopygium nearly reaching apex of metasoma (Fig. 32); male antenna with flagellar setae subequal to width of flagellomere (Fig. 46) [Costa Rica to Ecuador] . . . . . *ruficollis*
- Metafemur with dark spot, tarsal claws gracile; female with flagellum entirely dark; hypopygium reaching no more than ¾ length of metasoma (Fig. 41); male antenna with flagellar setae 2–3× width of flagellomere (male unknown in *B. citri*) (Fig. 51). . . . . 5

- 5(6) Larger ( $> 4$  mm); sides of gaster with extensive yellow markings, metacoxa entirely yellow (Fig. 4) [Costa Rica, Mexico] ..... *camacho*
- Smaller (3–4 mm); sides of gaster mostly black; metacoxa sometimes extensively black (Fig. 7) [Costa Rica] ..... *citri*
- 6(3) Scutellum mostly yellow or orange yellow (sometimes with a thin, longitudinal, black line in middle). ..... 7
- Scutellum entirely black. .... 10
- 7(6) Mesopleuron and propodeum black. .... 8
- Mesopleuron and propodeum orange (often black in median cavity). .... 9
- 8(7) Center of pronotum with wide black spot; dorsal-posterior part of head entirely black; mesoscutum and scutellum orange (reddish) yellow (Fig. 19) [Costa Rica] ... *ticos*
- Center of pronotum with very narrow, longitudinal black line; dorsal-posterior part of head with yellow area between occiput and ocellar area; mesoscutum and scutellum pale yellow (Fig. 2) [Brazil, Costa Rica] ..... *bahiae*
- 9(7) Top of head, dorsal surface of pronotum, and center of propodeum predominantly black; mesothorax reddish orange (Fig. 10) [Costa Rica] ..... *flava*
- Nearly entire body yellow (Fig. 3) [Ecuador] ..... *bouceki*
- 10(6) Lower face black, at least laterally, (Fig. 52) [small species, 4 mm or less in length; males unknown.] ..... 11
- Lower face completely yellow (Fig. 53). .... 12
- 11(10) Central area of lower face yellow (Fig. 52); entire mesosoma including coxae (at least basally) black; fore wing slightly infuscate below marginal and stigmal veins (Fig. 1); female petiole wider than long [Ecuador] ..... *atra*
- Entire head black; pronotum, pro- and mesocoxae yellow; fore wing not infuscate; female petiole at least  $3\times$  as long as broad (Fig. 13) [Ecuador] ..... *nigracephala*
- 12(10) Fore wing with dark spot beneath stigmal vein (Fig. 15) [Costa Rica] ..... *nublada*
- Fore wing without dark spot. .... 13
- 13(12) Gaster extremely narrow and elongate, in female length  $6\times$  maximum height (Fig. 11), in male at least  $3\times$  height; fore wing veins very thin (Fig. 54); mesoscutum and scutellum of male with transverse wrinkles, pronotum slightly concave dorsally. [Dorsal surface of mesosoma completely black] [Colombia, Ecuador, Peru, Venezuela] ..... *leptogaster*
- Gaster less elongate (length no more than  $5\times$  maximum height in female); veins thicker; male dorsum lacking above characteristics. .... 14
- 14(13) Gaster with continuous, longitudinal, pale stripe on lateral surface (not interrupted by vertical dark markings), more evident in female (Fig. 18) [Hypopygium nearly reaching tip of gaster, male scape without protruding apical knob, petiole predominantly smooth, dorsal surface of mesosoma entirely black, or nearly so] [Central, South America] ..... *stichogaster*
- Gaster without continuous pale stripe on lateral surface. .... 15
- 15(14) Metacoxa almost entirely black (Fig. 5) [Small, about 4 mm in length; mesosoma, except sides of pronotum, all black; male scape with apical knob opposite insertion of pedicel] [Brazil, Ecuador] ..... *chica*
- Metacoxa completely yellow. .... 16
- 16(15) Female with petiole elongate,  $4\times$  as long as wide (Fig. 55) [Size and color similar to *B. noyesi*; male unknown] [Ecuador] ..... *petiolata*
- Female with petiole at most as long as wide, usually wider than long. .... 17
- 17(16) Female petiole nearly as long as wide; male scape without apical knob, petiole slightly shorter than metacoxa and dorsally reticulate. [Small, about 4 mm in length; mesoscutum black, pronotum mostly yellow] [Colombia, Ecuador, Peru] ... *noyesi*
- Female petiole much wider than long; male scape with apical knob, or if without knob (*B. christeri*), then petiole slightly longer than metacoxa and dorsally shiny. .... 18



- 18(17) Female with pronotum usually entirely yellow (Fig. 6) (sometimes with some black posteriorly); mesoscutal lobes orange, antenna usually with pale funiculum and darker colored clava; male scape without pronounced apical knob. [Brazil, Colombia, Ecuador, Peru] ..... *christeri*
- Female pronotum with extensive black, mesoscutal lobes orange or black; antennal flagellum uniformly colored; male scape with prominent apical knob opposite insertion of pedicel (Fig. 56) [Colombia, Costa Rica, Ecuador, Peru, Venezuela] ..... *lorraineae*

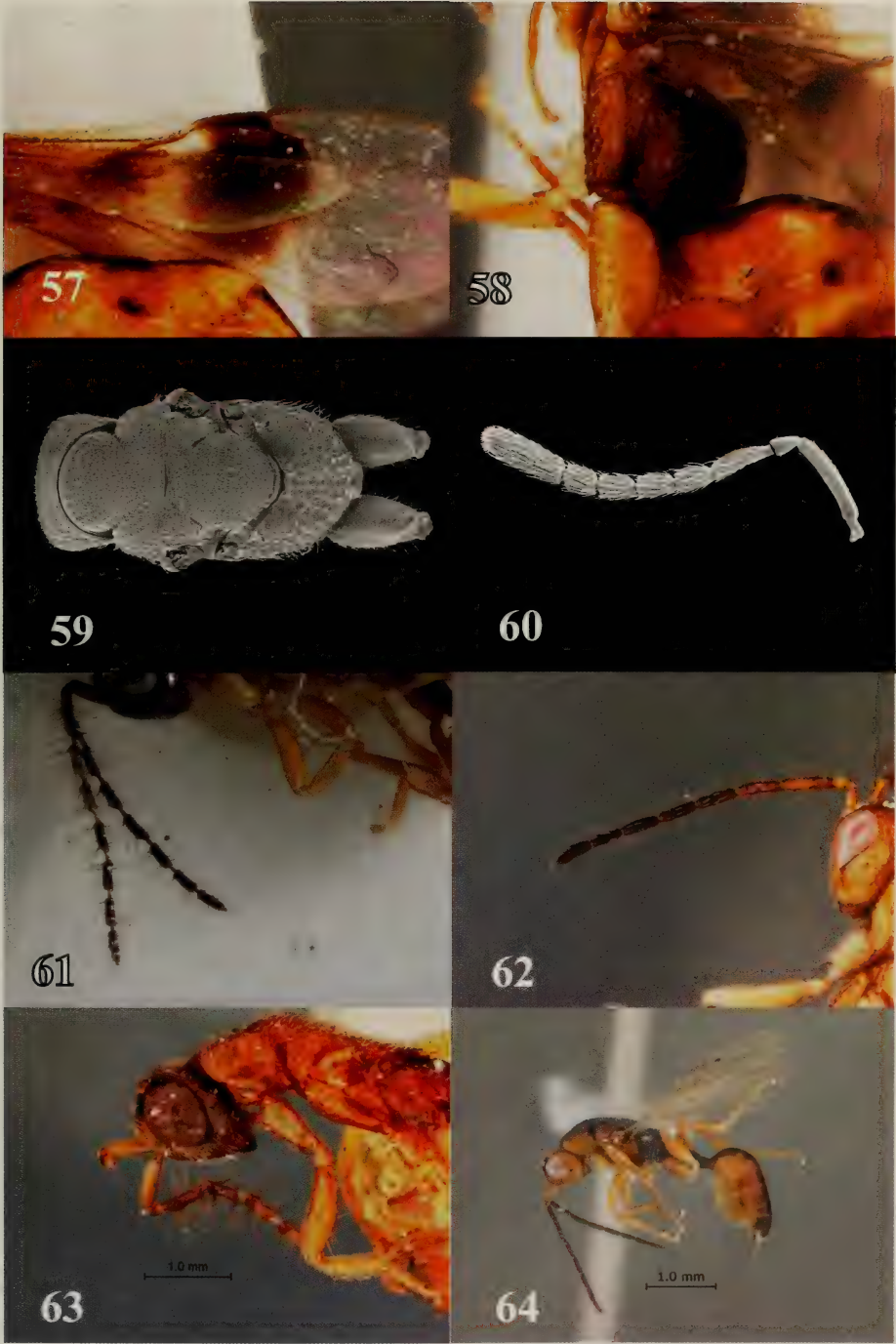
KEY TO SPECIES OF *ISOSOMODES*

- 1 Mesosoma with considerable orange coloration; male flagellomeres cylindrical or asymmetrical, their setae  $\geq 1.2\times$  longer than width of flagellomere ..... 2
- Body all dark brown to black (except for small yellow spot on anterior lateral corner of pronotum); male flagellomeres cylindrical, their setae  $\leq 1.1\times$  longer than width of flagellomere ..... 7
- 2(1) Scutellum orange ..... 3
- Scutellum black, at least posteriorly ..... 6
- 3(2) Fore wing with infusate spot (Fig. 57); propodeum with median channel deep, distinct, and reticulate (Fig. 58) [Ecuador] ..... *I. paradoxus*
- Fore wing hyaline; propodeum with median channel shallow, less distinct, and foveate (Fig. 59) ..... 4
- 4(3) Male flagellomeres symmetrical, either spindle-shaped or parallel-sided; female vertex and propodeum completely black ..... 5
- Male flagellomeres asymmetrical (Fig. 63); female unknown [Brazil] ..... *I. nigriceps*
- 5(4) Apex of female clava angled, with dense micropilosity (Fig. 60); head mostly black (Fig. 20); male antenna with flagellomeres asymmetrical, with long setae  $2-3\times$  as long as maximum diameter of flagellomere (Fig. 61) [Costa Rica]. ..... *I. azofiefai*
- Apex of female clava tapered, with sparser ring of micropilosity; head orange (Fig. 23); male antenna with flagellomeres parallel-sided, with long setae at most  $2\times$  as long as maximum diameter of flagellomere (Fig. 62) [USA: MD, NC]. ..... *I. landoni*
- 6(2) Apex of female clava tapered, with moderate micropilosity; mesoscutum and scutellum mostly black (Fig. 26); male antenna with flagellomeres parallel-sided, with long setae about as long as maximum diameter of flagellomere (Fig. 64) [USA: MD]. ..... *I. parkeri*
- Apex of female clava conical with dense micropilosity (Fig. 65); mesoscutum orange and scutellum black, at least posteriorly (Fig. 22); male antenna with flagellomeres spindle-shaped, with long setae  $2-3\times$  as long as maximum diameter of flagellomere (Fig. 66) [Colombia] ..... *I. colombia*
- 7(1) Female petiole  $<1.0\times$  as long as broad (Fig. 67); antenna with at least F6+clava brown, sometimes F2-F5 also brown; pro- and mesocoxae yellow or brown (Fig. 68); male flagellomeres brown (Fig. 69); petiole rugulose/foveolate dorsally, rarely with fine longitudinal carinae anteriorly, paired submedian carinae absent posteroventrally (Fig. 70) [USA, Central and South America]. ..... *I. gigantea*
- Female petiole  $>1.0\times$  as long as broad (Fig. 71); antenna with at least clava brown, F2-F5 yellow; pro- and mesocoxae yellow (Fig. 72); male flagellomeres yellow, except clava and F6 (often F5) brown (Fig. 73); petiole foveolate dorsally, with fine longitudinal carinae anteriorly, paired submedian carinae present posteroventrally (Fig. 74) [Costa Rica]. ..... *I. similis*

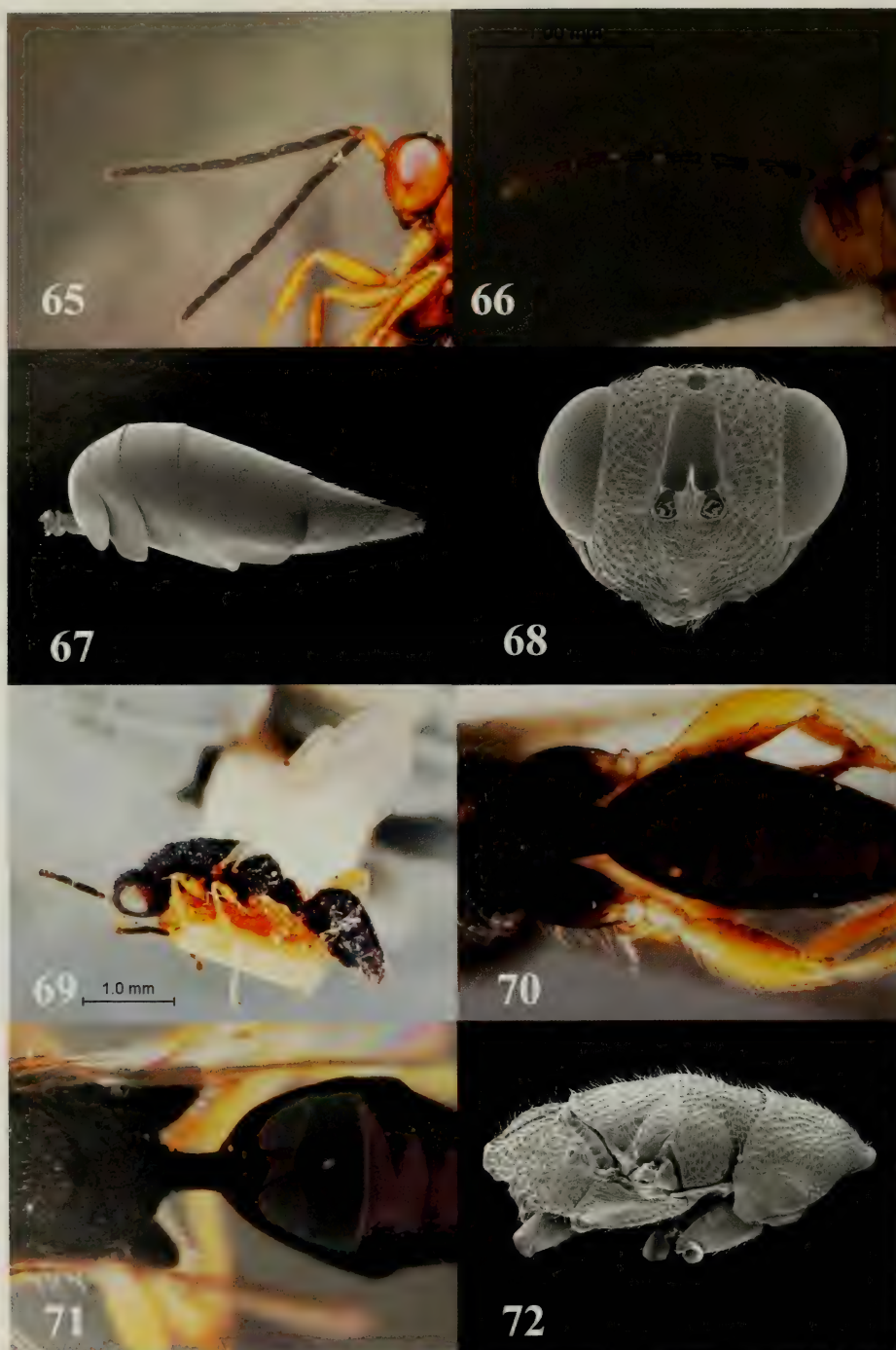


Figs 49–56. 49, *Bephrata cultriformis*, metatibial spur; 50, Pseudophyllinae eggs in *Citrus* stem (Tettigoniidae); 51, *B. camacho*, male antenna; 52, *B. atra*, face; 53, *B. nublada*, face; 54, *B. leptogaster*, fore wing; 55, *B. petiolata*, petiole; 56, *B. lorraineae*, male scape.





Figs 57–64. 57, *Isosmodes paradoxus*, fore wing; 58, *I. paradoxus*, propodeum; 59, *I. gigantea*, dorsal mesosoma; 60, *I. azofiefai*, female antenna; 61, *I. azofiefai*, male antenna; 62, *I. landoni*, male antenna; 63, *I. nigriceps*, male antenna; 64, *I. parkeri*, male habitus.



Figs 65–72. 65, *Isosmodes parkeri*, male antenna; 66, *I. colombia*, male antenna; 67, *I. gigantea*, female petiole; 68, *I. gigantea*, female habitus; 69, *I. gigantea*, male habitus, lectotype; 70, *I. gigantea*, male petiole; 71, *I. similis*, dorsal female petiole; 72, *I. similis*, female mesosoma.





Figs 73–79. 73, *Isosomodes similis*, male habitus; 74, *I. similis*, male dorsal petiole; 75, *I. azofiefai*, lateral mesosoma; 76, *I. azofiefai*, female fore wing; 77, *I. azofiefai*, ventral mesosoma; 78, *I. azofiefai*, male habitus; 79, *I. colombia*, female fore wing.

*Bephrata atra* Gates and Hanson, n. sp.  
(Figs 1, 52)

*Female holotype*.—Body length 3.5 mm. *Color*: Body black except yellow on lower scape (rest of antenna dark brown), central lower face (triangular area from toruli to lower margin of clypeus) (Fig. 52), fore and middle legs (coxae black), metatarsus; postorbital margin orange yellow; gaster partially yellowish brown laterally and ventrally (Fig. 1). *Head*: 1.4× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, extending 0.5× eye height; malar space 0.47× eye height; ratio of lateral ocellus: ocellular distance: postocellar distance as 15:13:35; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 21:10:1:18:14:14: 14:14:12:15. *Mesosoma*: 2.0× as long as broad, pronotum 0.7× as long as broad, mid lobe of mesoscutum about as long as broad, scutellum slightly longer than broad; notauli composed of row of foveae, axillular grooves obliterated; femoral depression substrigulate; metapleuron deeply foveate; propodeum deeply foveate to alveolate (with numerous carinae forming irregular setose cavities), with a broad, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a straight carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 62:22:12:7:4:7; ratio marginal vein: postmarginal vein: stigmal vein as 22:36:20, slightly infumate below marginal vein. *Mesosoma*: Petiole 0.35× as long as broad, gaster about 2.8× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 15:15:9:16:14:14:8:4; hypopygium reaching 0.75× length of gaster, apical region of ventral line with 6 pairs of setae.

*Male*.—Unknown.

*Diagnosis*.—Other small black species include *B. chica*, *B. citri*, and *B. nigracephala*.

However, *B. atra* is the only *Bephrata* having a black head with a yellow triangle on the lower face.

*Variation*.—Female length ranges 3.2–4.0 mm in length. The scape varies from yellow to dark brown, the pro- and mesocoxae vary from black to yellowish brown, and the degree of infumation on the fore wing is somewhat variable.

*Type specimens*.—Holotype, ♀ (USNM): ECUADOR, Napo, Reserva Etnica Waorani, Transect Ent. 1 km S. Okone Gare Camp, 00°39'10"S, 76°26'0"W, 220 m, 10.x.1994, T. Erwin et al., Canopy fogging, Lot # 942.

Paratypes, 3♀ (USNM): ECUADOR, same data as for holotype except 7.x.1995, Lot # 1233; Napo, Tiputini Biodiversity Station, 216 m, 00°37'55"S, 76°08'39"W, 7.ii.1999, T. Erwin et al., fogging of mostly bare green leaves, some with covering of lichenous or bryophytic plants, Lot # 2054, Transect 6 (2♀). PERU, Loreto, Cmp. S. Branch, 75.20W, 05.12E, Igagpo Forest, 12.v.1990, T. Erwin fogging to 20 m nr. river, Lethacidaceae + vine (♀).

*Etymology*.—From the Latin for black, referring to the predominantly black coloration of this species.

*Biology*.—Unknown.

*Distribution*.—Upper Amazon basin in Ecuador and Peru.

*Bephrata bahiae* (Ashmead)  
(Fig. 2)

*Aximogastra bahiae* Ashmead 1904: 261. Holotype ♀, by monotypy. Bahia, Brazil (USNM). *Bephrata bahiae*: Lotfalizadeh et al. 2007: 509.

*Female holotype*.—Body length 6.8 mm. *Color*: Yellow except following areas dark brown: transverse band on vertex between posterior ocelli, pronotum posteromedially, mesoscutum anteriorly, scutellum medially (line) and along posterior edge, dorsellum, propodeum, mesopleuron except along anterior edge femoral depression and dorsally, metapleuron except ovate area medially, petiole, Gt1, Gt2–3 with dorsal line and maculae at ventroposterior



corners, Gt4 with dorsal line expanded apically along tergal margin (T-shaped), Gt5–6 dorsally; syntergum, ovipositor sheaths. Head:  $1.3\times$  as broad as high; clypeus with apical margin emarginate; anterior tentorial pits indistinct; genal carina present, extending  $1/3$  eye height; malar space  $0.45\times$  eye height; ratio lateral ocellus:ocellocular distance:postocellar distance as 12:12:28; scape reaching just to anterior ocellus; ratio scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 38:15:3:30:20:[30:20:15:14:31: F3-club missing in LT]. Mesosoma:  $2.33\times$  as long as broad, pronotum  $0.50\times$  as long as broad, mid lobe of mesoscutum  $1.50\times$  as long as broad, scutellum  $1.40\times$  as long as broad; notauli and axillular grooves evident as row of foveae; femoral depression strongly substrigulate; metapleuron foveate; propodeum with numerous carinae forming irregular setose cavities, median channel broad, rugulose with a few cross carinae forming asetose cells; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina; [apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 130:25:25:14:8:20; missing in LT]; ratio marginal vein:postmarginal vein:stigmatal vein as 40:70:32. Metasoma: Petiole  $2.0\times$  broader than long, produced anterolaterally into small prongs; gaster nearly  $4\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 60:70:50:65:103:50:85:28; hypopygium nearly reaching  $0.85\times$  length of gaster, apical region of ventral line with 12 pairs of setae.

Male.—Body length 4.5 mm. Color: as described for female. Scape with concolorous oval area opposite insertion of pedicel, protruding as a knob; flagellomeres elongate and of uniform width, each with three whorls of erect setae, each 3– $4\times$  as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1–F6: clava as 35:10:2:40:36:33:31:30:25:30. Gastral petiole  $3.4\times$  as long as broad, just longer than metacoxa, nearly parallel-sided

but broadest medially, dorsally nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 55:20:22:29:24: 13:11:7.

Diagnosis.—Center of pronotum with very narrow, longitudinal black line; dorsal-posterior part of head with yellow area between occiput and ocellar area; mesoscutum and scutellum pale yellow. *Bephrata bahiae* may be confused with *B. ticos*, but the latter species has the center of pronotum with wide black spot, the dorsal-posterior part of head entirely black, and the mesoscutum and scutellum orange (reddish) yellow.

Variation.—Females vary in the extensiveness of the dorsal maculation and wing infuscation. One specimen from Cabo Blanco has a darker brown flagellum than the second from that locality.

Type specimens.—Holotype, ♀ (USNM): 789, Bahia, Brazil, Type No. 7342.

Other specimens examined.—COLOMBIA, Bolivar SFF, Los Colorados, La Suiris,  $9^{\circ}54'00''\text{N}$   $75^{\circ}07'00''\text{W}$ , 126 m, 15–30.ix.2000, E. Deuluteut (1♂, USNM). COSTA RICA, Limon, Parque Nacional Tortuguero, Estación Cuatro Esquinas, 0 m, iv.1993, R. Delgado, LN 280000 590500 (1♀, MZCR); Puntarenas, Estación Cabo Blanco, 100 m, 18.vii–9.x.1991, Malaise, LN 175150 416300, #1873, COSTA RICA INBio CRI00061926478 (1♀, INBio); Reserva Natural Cabo Blanco, Estación San Miguel, ix.1993, M. Ramírez, LS 173174\_411412, #2343, COSTA RICA INBio CRI00061651456 (1♀, INBio).

Biology.—Unknown.

Distribution.—Known from Brazil, Colombia, and Costa Rica.

*Bephrata bouceki* Gates and Hanson, **n. sp.**  
(Fig. 3)

Female holotype.—Body length 7.6 mm. Color: Yellow except following areas dark brown: F6, clava, medial margin posterior ocellus, posterior margin anterior ocellus, petiole, longitudinal median strip on anterior  $1/2$  Gt1, dorsoapical macula medially on Gt2, dorsoapical macula ( $\Delta$ -shaped) medially on Gt3, dorsoapical macula ( $\Delta$ -

shaped) medially on Gt4 becoming transverse band laterally, Gt5 dorsally (faint); ovipositor sheaths. Fore wing weakly infusate near venation and in basal 1/3. Head: 1.4× as broad as high; clypeus with apical margin emarginate; anterior tentorial pits small; genal carina present, extending 1/3 eye height; ratio lateral ocellus:ocellocular distance:postocellar distance as 13:11:25; scape extending above anterior ocellus; ratio scape (minus radicle):pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 50:17:3:41:32:31:30:28:23:34. Mesosoma: 2.0× as long as broad, pronotum 0.66× as long as broad, mid lobe of mesoscutum 1.56× as long as broad, scutellum about as long as broad; notauli weak but evident, axillular grooves evident; femoral depression strigulate; metapleuron foveate-alveolate; propodeum with numerous carinae forming irregular setose cavities, median channel broad, nitid, lacking transverse carinae; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina; apex of metatibia with a short, pointed spur; ratio metatibia: metatarsomeres as 170:55:28:15:10:25; ratio marginal vein:postmarginal vein:stigmatal vein as 55:90:48. Metasoma: Petiole 0.2× as long as broad, produced laterally as upturned spur; gaster nearly 3.5× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 45:110:70:90:100:55:40:10; hypopygium nearly reaching 0.90× length of gaster, apical region of ventral line with 10 pairs of setae.

Male.—Body length 5.7 mm. Color: as described for female, except dorsum of gaster black and petiole dark brown. Scape with pale oval area opposite insertion of pedicel, protruding as a knob; flagellomeres elongate and of uniform width, each with multiple whorls of erect setae, each 2–4× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1–F6: clava as 50:13:2:50:50:47:40:40:35:40. Gastral petiole 4.0× as long as broad, just longer than metacoxa, nearly parallel-sided but broadest medially, dor-

sally nitid, ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 75:20:22:29:24:13:11:7.

Diagnosis.—This is one of the only nearly uniformly yellow species, comparable to *B. flava*, but that species has the propodeum, vertex, and dorsal pronotum black.

Variation.—The four known females are very similar, length ranges 4–7.6 mm.

Type specimens.—Holotype, ♀ (USNM): ECUADOR, Sucumbios, Sacha Lodge, 0.5°S 76.5°W, 10–20.ix.1994, P. Hibbs, MT.

Paratypes, 3♀, 1♂: same data as holotype (1♀, USNM); Napo, 1 km S. Okonegare Camp, Reserva Etnica Waorani, 220 m, 22.vi.1998, 00° 39'10"S 76° 26'00"W, T. L. Erwin et al., fogging terre firme forest, transect Ent Lot 715 (1♀, EPNC). COLOMBIA, Amazonas, Productividad Primaria Neta Amacayacu Matatmata, Mocagua, 300 m, 24.iv–5.v.2000, 3° 23'01"N 70° 06'01"W, A. Parente, M.88 (1♂, IAVH). PERU, Madre de Dios, Rio Tambopata Res., 30 km (air) SW Puerto Maldonado, 290 m, 10.ix.1984, 12° 50'S 69° 17'W, Smithsonian Institution Canopy Fogging Project, T. L. Erwin (1♀, USNM).

Etymology.—Named for Zdenek Bořček in honor of his massive contributions to the study of Chalcidoidea.

Biology.—Host unknown.

Distribution.—Colombia, Ecuador.

*Bephrata camacho* Gates and Hanson, **n. sp.** (Figs 4, 41, 51)

Female holotype.—Body length 5.8 mm. Color: Head orange yellow, antennal flagellum dark brown, small black area in ocellar area and occiput; mesosoma black except yellow on lateral dorsal margin and lateral margin of pronotum; legs yellow except dark spot on basal 1/2 of metafemur; gaster with terga 1–2 and 6–7 dark brown, Gt3–Gt5 light yellow except dark brown dorsally (medially) and with much broader band on posterior margin. Head: 1.4× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, extending 1/3 eye height; malar space 0.31× eye height; ratio of lateral ocellus: ocellocular distance:



postocellar distance as 11:4:17; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: clava as 30:5:2:22:19:19:17:15:14:16. Mesosoma: 2.3× as long as broad, pronotum 0.7× as long as broad, mid lobe of mesoscutum and scutellum approximately as long as broad; notauli and axillular grooves obliterated; femoral depression coriarius-substrigulate; metapleuron deeply foveate to alveolate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with shallow, narrow groove in center; basal anterior portion of procoxa with large oblique depression, bordered mesally by semicircular carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 47:20:9:6:3:5; ratio marginal vein: postmarginal vein: stigmal vein as 24:35:14. Metasoma: Petiole 0.5× as long as broad, produced laterally as upturned spurs; gaster 3.4× as long as high; ratio of Gt1-Gt7, ovipositor sheath (all measured dorsally): 20:13:21:28:19:32:13:6; hypopygium reaching 0.6× length of gaster, apical region of ventral line with 10 pairs of setae.

*Male*.—Body length 3.8 to 5.4 mm. Color: as for female, except often with more black on top of head, pronotum, and dorsal (medial) part of terga. Scape with light colored oval area opposite insertion of pedicel, but this area not protruding as a knob; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 30:7:2:36:35:33:32: 28:24:28. Gastral petiole 3.5× as long as broad, same length as metacoxa, nearly parallel-sided but narrowing slightly at apex, dorsal surface coriarius; ratio of petiole: Gt1-Gt7 (dorsal length measured in lateral view) as 30:23:7:20:24:18:8:11.

*Diagnosis*.—This species and *B. ruficollis* are the only two *Bephrata* with a completely light-colored metatibia. However, *B. camacho* has lighter yellow markings as opposed

to orange yellow, has a dark spot on the metatibia, the female flagellum is uniformly colored, the hypopygium barely reaches beyond the midpoint of the gaster, and the flagellar setae of the male are much longer.

*Variation*.—Female length ranges 4.0–6.1 mm in length. Specimens vary in the amount of black markings on the top of the head and pronotum, from relatively little to extensive (as in males).

*Type specimens*.—Holotype, ♀ (USNM): COSTA RICA, Heredia, OTS-La Selva, 100 m, iii–iv.1993, P. Hanson, MT.

Paratypes, 61♀, 24♂: Same data as for holotype (1♀, USNM); iii.1991 (2♀, CNC); iv.1991 (3♀, CNC); ix.1992 (2♀, 1♂, CNC); v.1990, H. Hespeneheide (1♀, 1♂, USNM); i.1994, ALAS (3♀, USNM); ii.1994 (1♀, USNM); ix.1994 (1♀, USNM); 30.iii.2002, M. Gates (1♂, USNM); Heredia, Chilamate, 75 m, vii–viii.1989, P. Hanson (1♂, USNM); Puntarenas, San Vito, Jardin Bot. Las Cruces, 1200 m, vi–vii.1988, P. Hanson (1♀, 2♂, MZCR); vii–viii.1988 (4♀, 1♂, USNM); Estación Biológica Las Alturas, 1500 m, i.1992, Hanson and Godoy (1♀, USNM); v.1992 (2♀, 2♂, USNM); vi.1992 (1♀, USNM); xi–xii.1992 (1♂, USNM); Puntarenas, Reserva Biológica Carara, Estación Quebrada Bonita, 50 m, v–vi.1989, P. Hanson (1♂, USNM); Golfo Dulce, 10 km W Piedras Blancas, 100 m, iii–v.1989, P. Hanson (1♀, 1♂, USNM); 24 km W Piedras Blancas, 200 m, ii–iii.1989 (2♀, MZCR); iii–iv.1989 (1♀, MZCR); vi–vii, 1989 (1♀, MZCR); iii–vi.1990 (1♀, MZCR); vii–ix.1990 (1♀, MZCR); iv–v, 1991 (2♀, MZCR); ii.1992 (2♀, MZCR); 3 km SW Rincon, 10 m, iii–v.1989 (2♀, MZCR); vi–viii.1989 (3♀, MZCR); iii.1993 (2♀, MZCR); Parque Nacional Corcovado, Estación Los Patos, Sendero Sirena, El Pavo, 70 m, 13.ii–18.iii.2001, J. Azofeifa (1♀, INBio); Guanacaste, Estación Pitilla, 9 km S Santa Cecilia, 700 m, v.1988, P. Hanson and I. Gauld (1♀, 1♂, BMNH); ix.1988 (5♀, 1♂, BMNH); i.1989 (1♀, BMNH); iv.1989 (2♀, 1♂, BMNH); v.1989 (2♂, BMNH); vi.1989 (4♀, BMNH); Guanacaste, Estación Maritza, W. Volcan Orosi, iv–v.1989 (1♀, 1♂, INBio); Guanacaste, Macizo Miravalles, Estación Cabro Muco, 1100 m, iii.2003, J. Azofeifa, B. Hernandez, J.D. Gutierrez (1♀, 2♂, INBio); Alajuela, San Carlos, La Fortuna, Parque Nacional Arenal, Sector Catarata, 500 m, 15.iii–24.iv.2001, G. Carballo (1♀, INBio). MEXICO, Veracruz, Estación Biológica De Los

Tuxtla, 18°35'N 95°05'W, 28.iv.1991, H. A. Hespenheide (4♂, USNM); 7.v.1991 (1♀, USNM); Quintana Roo, Chichén Itzá Ruins, 17.xii.93, L. Masner (1♀, USNM); San Antonio port of entry, July 14 1956, ex *Chamaedorea* stem (1♀, USNM).

*Etymology*.—Named in honor of Eddy Camacho for his numerous roles in assuring the efficient operation of lab 170 (Entomology) in the Escuela de Biología, Universidad de Costa Rica.

*Biology*.—Host unknown. One specimen from Mexico intercepted at the port-of-entry in San Antonio was apparently reared from a palm stem ("ex *Chamaedorea* stem"). A specimen from Costa Rica (La Selva, 9.v.1990, H. Hespenheide) is labeled "Clusia TF". This is one of the most commonly collected species of *Bephrata* in Costa Rica; specimens have been obtained from Malaise traps, sweeping, yellow pan traps, and canopy fogging.

*Distribution*.—Costa Rica (sea level to 1200 m), Mexico (Veracruz, Quintana Roo).

*Bephrata chica* Gates and Hanson, n. sp.  
(Fig. 5)

*Female holotype*.—Body length 3.7 mm. Color: Body black except yellow on lower face and gena, lateral surface of pronotum, fore and middle legs, metatarsus; antenna and metafemur yellowish brown; gaster partially yellowish brown laterally and ventrally. Head: 1.2× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, extending 0.5× eye height; malar space 0.44× eye height; ratio of lateral ocellus: ocellular distance: postocellar distance as 13:15:36; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: clava as 20:9:2:16:14:13:13:13:10:16. Mesosoma: 2.0× as long as broad, pronotum 0.7× as long as broad, mid lobe of mesoscutum about as long as broad, scutellum slightly longer than broad; notauli present as a row of foveae and axillular grooves deep; femoral depression coriarius-substrigulate; meta-

pleuron deeply foveate; propodeum deeply foveate to alveolate (with numerous carinae forming irregular setose cavities), with a broad, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a heavily sclerotized sinuous carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 57:21:11:9:4:10; ratio marginal vein: postmarginal vein: stigmal vein as 22:35:21. Metasoma: Petiole 0.35× as long as broad, gaster about 3× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 20:13:8:16:15:8:11:3; hypopygium reaching 0.8× length of gaster, apical region of ventral line with 6 pairs of setae.

*Male*.—Body length 2.8–4.0 mm. Color as for female, except often with more black on top of head, pronotum, and dorsal (medial) part of terga. Scape with whitish protruding knob opposite insertion of pedicel; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 21:4:2:20:22:22:20:17:12:16. Gastral petiole 4.0× as long as broad, 1.1× length of metacoxa, nearly parallel-sided, dorsal surface nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 20:18:10:12:8:3:7:3.

*Diagnosis*.—Like *B. atra*, *B. citri*, and *B. nigracephala*, this is a small black species. However, *B. chica* can be distinguished by its black hind legs (except for the tarsi) and yellow lower face.

*Variation*.—Female length ranges 3.7–4.3 mm in length. On the head, the region between the ocelli and the occiput may be either solid black, or there may be two black areas separated by orange yellow.

*Type specimens*.—Holotype, ♀ (USNM): ECUADOR, Napo, Reserva Etnica Waorani, Transect Ent. 1 km S. Okone Gare Camp, 00°39'10"S 76°26'0", 220 m, 8.x.1995, T. Erwin et al., Canopy fogging, t10.5 #1265.



Paratypes, 2♀, 7♂ (USNM): same data as for holotype except 00°39'25.7"S 76°27'10.8"W, 216.3 m (1♂); Napo, Tiputini, Biodiversity Station, 216 m, 00°37'55"S 76°08'39"W, 22.x.1998, Lot # 1960 (1♂); 23.x.1998, Lot # 1900 (1♂); 5.ii.1999, Lot # 2090 (1♂). PERU, Madre de Dios, Rio Tambopata Res., 30 km (air) SW Puerto Maldonado, 290 m, 12°50'S 69°17'W, 12.xi.1983, T. Erwin (1♀); same data except 10.ix.1994 (1♂); Peru, Miami port of entry, 7.v.1964, with orchid, J. C. Buff (1♂). BRAZIL, Amazonas, 18.1 km E Campinas field station, km 60, N Manaus, 22.ii.1979, 02°30'S 60°15'W, canopy fogging sample #22, Montgomery et al. (1♀); Brazil, 29.x.1940, on bromeliads, Lot No. 40-22688 (1♂).

**Etymology.**—From the Spanish for small, referring to the diminutive size of this species.

**Biology.**—Unknown. One specimen was collected in association with an orchid and another with bromeliads.

**Distribution.**—Amazon basin of Brazil, Ecuador, and Peru.

*Bephrata christeri* Gates and Hanson, n. sp.  
(Fig. 6)

**Female holotype.**—Body length 4.4 mm. **Color:** Head yellow except black on last two flagellomeres and small area around ocelli; mesosoma black except yellow pronotum and legs (metatibia dark brown), mesoscutal lobes orange (reddish) yellow; petiole black, gaster yellow except terga 1 and 7 dark brown, Gt3–Gt6 dark brown medially at dorsoposterior margin, especially Gt4 where dark band extends very far laterally (ventrally). **Head:** 1.4× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, extending 1/3 eye height; malar space 0.29× eye height; ratio of lateral ocellus: ocellocular distance: post-ocellar distance as 21:11:36; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: clava as 30:10:2:27:23:23:22:21:17:25. **Mesosoma:** 2.1× as long as broad, pronotum 0.7× as long as broad, mid lobe of mesoscutum and

scutellum about as long as broad; notauli and axillular grooves as rows of shallow foveae; femoral depression substrigulate; metapleuron deeply foveate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a broad, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina somewhat laminate distally; apex of metatibia with a short, pointed spur; ratio metatibia: metatarsomeres as 46:18:9:6:4:6; ratio marginal vein: postmarginal vein: stigmal vein as 35:59:29. **Metasoma:** Petiole very transverse, gaster 2.2× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:25:15:30:23:4:9:4; hypopygium reaching 0.9× length of gaster, apical region of ventral line with 6 pairs of setae.

**Male.**—Body length 3.8–4.1 mm. **Color:** as for female, except antenna dark brown, entire ocellar area and dorsal surface of pronotum black, and gaster with more dark markings. Scape with whitish oval area opposite insertion of pedicel, but hardly protruding; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 15:3:1:14:14:15:14:14:11:13. Gastral petiole 3.9× as long as broad, 1.1× length of metacoxa, nearly parallel-sided, dorsal surface nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 24:20:19:15:16:17:11:3.

**Diagnosis.**—This species is quite similar to *B. lorraineae*, but the latter species usually has more extensive black coloration on the pronotum and the female antennal flagellum is uniformly colored (as opposed to bicolored in *B. christeri*). The male scape of *B. lorraineae* has a prominent knob near the apex, which is much less well developed in *B. christeri*.

**Variation.**—Female length ranges 4.4–7 mm in length. The amount of black in

the ocellar region varies but never extends back to the occiput. Also somewhat variable is the degree to which the last two flagellomeres are darker than the preceding ones.

*Type specimens*.—Holotype, ♀ (USNM): ECUADOR, Napo, Reserva Etnica Waorani, Transect Ent. 1 km S. Okone Gare Camp, 00°39'10"S 76°26'0", 220 m, 10.ii.1995, T. Erwin et al., Canopy fogging, Lot #1009, t8...10 tierra firme forest.

Paratypes, 12♀, 6♂ (USNM): same data as holotype (2♀), same data except 10.x.1994, Lot 941 (1♀); 9.x.1995, Lot 1193 (1♀); 7.ii.1996, Lot 1443 (1♂); 216.3 m, 00°39'25.7"S 76°27'10.8"W, 6.x.1995, #1225 (1♀); 7.x.1995, #1240 (2♀); 12.ii.1995, #1033 (1♂); Tiputini Biodiversity Station, 216 m, 00°37'55"S 76°08'39"W, 5.ii.1999, Lot 2086, Trans 9 (1♂); 1.vii.1999, Lot 1852, Trans 6 (1♀). COLOMBIA, Amazonas, Productividad Primaria Neta Amacayacu, Matamata, San Martin, 150 m, 3°23'01"N 76°06'01"W, 30.vii–8.viii.2000, B. Amado, M.836 (1♀); 17–30.vii.2000, M.701 (1♂); 6–12.vi.2000, M.696 (1♂); 16–24.ix.2000, M.840 (1♂); Caqueta, Parque Nacional Natural Chiribiquete, Rio Sararamana, 0°9'44"N 72°37'01"W, 9–13.iv.2000, J. Cantillo, #484 (1♀); PERU, Madre de Dios, Rio Tambopato Res., 30 km (air), SW Puerto Maldohnado, 290 m, 12°50'S 69°17'W, 10.ix.1984, T. Erwin (1♀). BRAZIL, Amazonas, Hwy. ZF 2, km 19, ca 60 km N Manaus, 02°30'S 60°15'W, 17.viii.1979, Terra firme, canopy fogging TRS#09, tray# 632, Adis et al. (1♀).

*Etymology*.—Named in honor of Christer Hansson, for his contributions to our knowledge of Neotropical Chalcidoidea.

*Biology*.—Unknown.

*Distribution*.—Amazon basin of Brazil, Colombia, Ecuador, and Peru.

*Bephrata citri* Gates and Hanson, n. sp.  
(Figs 7, 40)

*Female holotype*.—Body length 4.2 mm. *Color*: Black except following areas yellow: scape, apical 1/3 pedicel, anellus, face, gena, lateral panel pronotum, tegula, fore and middle legs, apical 1/3 metacoxa, metatrochanter, apical fifth metafemur, metatibia, and metatarsus. *Head*: 1.3× as broad as high; clypeus with apical margin

shallowly notched medially; anterior tentorial pits evident; striae radiating from clypeus very weak; genal carina present, extending to 0.5× eye height; malar space 0.4× eye height; ratio lateral ocellus:ocellular distance:postocellar distance as 5:7:23; scape reaching just to anterior ocellus; ratio scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 25:8:2:18:17:16: 14:13:10:30. *Mesosoma*: 2.1× as long as broad, pronotum 0.6× as long as broad, mid lobe of mesoscutum 1.3× as long as broad, scutellum 1.3× as long broad; notauli as row of foveae and axillular grooves obliterated; femoral depression coriarius; metapleuron foveate; propodeum with numerous carinae forming irregular setose cavities, median channel narrow, with transverse carinae; basal anterior surface of procoxa with large oblique depression, bordered mesally by a short convex carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 78:33:7:8:6:10; ratio marginal vein:postmarginal vein:stigmatal vein as 35:60:31. *Metasoma*: Petiole with dorsal length 0.7× as long as broad, produced anterolaterally into dull prongs; gaster about 3× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 35:26:18:29:40:41:20:4; [hypopygium nearly reaching 0.5× length of gaster, apical region of ventral line with 3 pairs of setae].

*Male*.—Unknown.

*Diagnosis*.—Like *B. atra* and *B. nigracephala*, this is a small black species. However, *B. citri* can be distinguished by its yellow metatibiae.

*Variation*.—Female length ranges 4.2–4.3 mm. In the paratype, the gaster is slightly more yellow ventrally.

*Type specimens*.—Holotype, ♀ (USNM): COSTA RICA, Puntarenas, San Vito de Coto Brus, V.1990, Luis More, huevos en tallo de citrico.

Paratypes, 3♀: same data as holotype (2♀, BMNH, USNM); Alajuela, Chiles de Aguas Zarcas, cafe, 300 m, i.1990, R. Cespedes (1♀, MZCR).



*Etymology*.—This species is named for the genus of plant with which the holotype is associated.

*Biology*.—Reared from eggs of pseudophylline katydids (Orthoptera: Tettigoniidae) embedded in citrus stems.

*Distribution*.—Costa Rica.

*Bephrata clava* Gates and Hanson, **n. sp.**  
(Fig. 8)

*Female holotype*.—Body length 7.2 mm. *Color*: Orangish yellow except black mandibular teeth, ocellar area, metatibia, central concavity of propodeum, and gastral petiole; antennal pedicel and flagellum dark brown; gaster with terga 1 and 7 dark brown, Gt2–Gt6 with broad dark brown bands posterior dorsally. *Head*: 1.3× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina absent; malar space 0.34× eye height; ratio of lateral ocellus: ocellocular distance: postocellar distance as 13:9:20; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 38:12:3:27:25:25:22:21:18:27. *Mesosoma*: 1.8× as long as broad, pronotum 0.6× as long as broad, mid lobe of mesoscutum 1.1× as long as broad, scutellum approximately as long as broad; notauli evident as dark lines beneath surface sculpture, axillular grooves evident as row of foveae; femoral depression coriarius, adscrobal carina obliterated; metapleuron alveolate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with deep, broad, weakly sculptured median channel; basal anterior portion of procoxa without large oblique depression; apex of metatibia with a short, blunt spur; ratio metatibia: metatarsomeres as 62:41:20:11:4:9; ratio marginal vein: postmarginal vein: stigmal vein as 35:43:22. *Metasoma*: Petiole transverse and barely visible, gaster very elongate, about 4× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 22:56:42:38:45:18:18:6; hypopygium reaching almost to

tip of gaster, apical region of ventral line with 11 pairs of setae.

*Male*.—Body length 5.3–6.3 mm. *Color*: as for female. Scape with protruding knob at apex, opposite insertion of pedicel; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 32:7:2:38:36:35:33:30:30:32. Gastral petiole 4.4× as long as broad, 1.2× length of metacoxa, nearly parallel-sided, dorsal surface coriarius; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 35:27:30:38:25:15:15:12.

*Diagnosis*.—This species and *B. cultriformis* are the only species in the genus that lack the distinctive groove on the procoxae and could therefore be misidentified as a species of *Isosomodes*, but both can be distinguished from this genus by the characters listed in Table 1. *Bephrata clava* can be distinguished from *B. cultriformis* by its very different coloration, described above.

*Variation*.—Little variation was seen in the two females and two males examined.

*Type specimens*.—Holotype, ♀ (USNM): COSTA RICA, Heredia Pr, La Selva Biológica Sta., 3 km S Pto. Viejo, 10°26'N 84°01'W, 8.viii.1992, H. A. Hespenheide.

Paratypes, 1♀, 2♂: COSTA RICA, Guanacaste, Estación Maritza, W. Volcan Orosi, 600 m, vi.1988 (1♂, USNM); Estación Maritza, W. side Volcan Orosi, 600 m, 1989, GNP Biodiversity Survey, Malaise L\_N\_326900\_373000 #6834 (1♀, MZCR); Limon, Parque Nacional Tortugero, Cuatro Esquinas, 0 m, xii.1992, R. Delgado (1♂, INBio).

*Etymology*.—From the Latin *clava* meaning club, referring to the stubby spur at the apex of the metatibia.

*Biology*.—Unknown.

*Distribution*.—Costa Rica, from sea level to 600 m.

*Bephrata cultriformis* (Ashmead)  
(Figs 9, 47–49)

*Bephrata cultriformis* Ashmead 1894: 146. Holotype ♀, by monotypy. St. Vincent (USNM).

*Aximogastra cultriformis*: Gahan 1951: 173.

*Bephrata cultriformis*: Lotfalizadeh et al. 2007: 508.

*Female lectotype*.—Body length 6.3 mm. Color: yellow except following areas dark brown: antenna, metatibia except apices, Gt1, Gt2–5 with dorsal line that is expanded apically along tergal margin ( $\Lambda$ -shaped) and extending laterally, Gt6 dorsally; syntergum, ovipositor sheaths; or black: vertex transversely encompassing ocelli, just dorsad occipital foramen, pronotum posteromedially, mesoscutum anteriorly and with medial stripe, notauli, scutellum, dorsellum, propodeum, petiole. Head:  $2.1\times$  as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina absent; malar space  $0.3\times$  eye height; ratio lateral ocellus:ocellocular distance: postocellar distance as [12:12:28; rest of antenna covered in glue in holotype]; scape reaching to anterior ocellus; ratio scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 34:13:2:27:21:23:20: [15:14:31; missing in holotype]. Mesosoma:  $2.3\times$  as long as broad, pronotum  $0.7\times$  as long as broad, [mid lobe of mesoscutum  $1.5\times$  as long as broad; glued in holotype], scutellum just longer than broad; notauli as rows of foveae, axillular grooves evident as impressed lines; femoral depression coriarius; metapleuron foveate; propodeum with numerous carinae forming irregular setose cavities, median channel broad, rugulose-reticulate with a few cross carinae along midline; procoxa rounded anterobasally, without a channel-like arcuate depression; apex of metatibia with a short spur blunt; ratio metatibia: metatarsomeres as 110:60:32:28:9:20; ratio marginal vein: postmarginal vein: stigmal vein as 60:80:38. Metasoma: Petiole  $0.5\times$  as long as broad, unproduced anterolaterally; gaster about  $4.7\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 80:80:75:70:35:30:13:10; [hypopygium nearly reaching  $0.85\times$  length of gaster, apical region of ventral line with 12 pairs of setae].

*Male*.—Body length 5.1 mm. Color: as in female, but dark coloration on gaster more extensive (see Variation); Scape with concolorous oval area opposite insertion of pedicel, protruding as a knob; flagellomeres elongate and of uniform width, evenly covered with multiple whorls of erect setae, each  $2\text{--}3\times$  as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 38:10:2:40:40:40:35:30:28:35. Gastral petiole  $5.0\times$  as long as broad, just longer than metacoxa, nearly parallel-sided but broadest medially, dorsally nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 75:20:30:40:40:35:18:5.

*Diagnosis*.—This species and *B. clava* are the only species in the genus that lack the distinctive groove on the procoxae and could therefore be misidentified as *Isosomodes*, but both can be distinguished from this genus by the characters listed in Table 1. *Bephrata cultriformis* can be distinguished from *B. clava* by its very different coloration described above.

*Variation*.—Female length ranges 5–10 mm and males 4.0–6.3 mm. Both sexes vary considerably in extent of darker maculation on the body. The female from Venezuela has the lightest maculation, consisting of dark brown areas just surrounding the ocelli, a narrow stripe spanning the posteromedial pronotum and anteromedial mesoscutum, along the notauli in part and axillular grooves, mesopleuron, metapleuron, propodeum, metatibiae, metatarsomeres (light brown), petiole, and gaster (as in description). In the darkest female (Valle de la Estrella), not only is the maculation darker, but it is more extensive as follows: entire vertex and part of scrobal depression, subocular spot, occipital region, entire collum and medial  $1/3$  pronotum, mesoscutum except strip along notauli, length of notauli, and the remainder as in Venezuela specimen but darker. The Ecuadorean females have maculation, in addition, as follows: supraclypeal spot, metacoxa in posterior  $1/2$ , metafemur



except apices. Males exhibit very similar color variation, though the least maculated specimens are not equal to that seen in the female from Venezuela.

*Type specimen*.—Holotype, ♀ (USNM): 2000 feet, St. Vincent, W. I., H. H. Smith, Paratype No. 2424 USNM. Described from a single specimen.

*Other specimens examined*.—COSTA RICA, Heredia, F. La Selva, 3 km S Puerto Viejo, 10° 26'N 84°01'W, 26.vi.1985, H. A. Hespenheide (1♀, USNM); Heredia, 3 km S Puerto Viejo, OTS-La Selva, 100 m, x.1992, P. Hanson (1♀, MZCR); OTS-La Selva, iii–iv.1993 (1♀, USNM); Limón, Valle de la Estrella, Reserva Biológica Hitoy Cerere, Sendero Toma de Agua, 100 m, 17.iv–8.v.1999, F. Umaña. Malaise L\_N\_184600\_643400, #52757 (1♀, INBio). DOMINICA, Dleau Gommier, 1400', 2.iii.1965, H. E. Evans, Bredin-Archbold-Smithsonian Bio. Surv. Dominica (1♂, USNM). ECUADOR, Napo, 1 km S. Okonegare Camp, Reserva Etnica Waorani, Transect Ent, 220 m, 2.vii.1995, 00° 39'10"S 76° 26'00"W, T. L. Erwin et al., canopy fogging, Lot #1063, t7.3 terre firme forest, Restrictions Apply NMH-DCB/EPN Agreement 39 (1♂, EPNC); same data as previous but different dates/lots: 2.vii.1995, Lot #1090, t6..10 (1♂, EPNC); 9.vii.1995, Lot #1151 (2♂, EPNC); 5.x.1995, Lot #1194, t3.4 (2♂, EPNC); 6.x.1995, Lot #1223 (1♀, EPNC); 8.x.1995, Lot #1261 (1♀, EPNC); 8.x.1995, Lot #1265, t10.5 (1♂, EPNC); 7.ii.1996, Lot #1443, t5..3 (1♂, EPNC). MEXICO, Veracruz, Estación Biológica de Los Tuxtlas, 18°35'N 95°05'W, 28.iv.1991, H. A. Hespenheide (2♂, USNM); PERU, Madre de Dios, Rio Tambopata Res., 30 km (air) SW Puerto Maldonado, 290 m, 14.ix.1984, 12° 50'S 69° 17'W, T. Erwin et al. (1♀, USNM). VENEZUELA, San Esteban, xi.1939, Pablo Anduze (1♀, USNM).

*Biology*.—Host unknown. Two females from La Selva, Costa Rica, have mites on the gaster; one of them (collected 26.vi.1985) had nearly 40 individuals.

*Distribution*.—Costa Rica, Dominica, Ecuador, Mexico (Veracruz), Peru, and Venezuela.

*Bephrata flava* Gates and Hanson, **n. sp.**  
(Fig. 10)

*Female holotype*.—Body length 5.9 mm. Color: Head yellow except black from vertex (beginning in upper 1/2 of antennal scrobe) to back of head and a small spot

below eye; antennal pedicel and flagellum dark brown; mesosoma orange yellow except black on dorsal pronotum, central cavity of propodeum, and metasternum, side of pronotum yellow; legs yellow except metatibia black; petiole black; gaster yellow except terga 1 and 7 dark brown, Gt3–Gt6 dark brown dorsally (medially) with posterior band extending ventrally (laterally) on Gt4 and Gt5, Gt3 with ventral band. Head: 1.3× as broad as high; clypeus with apical margin straight, curved slightly inward; anterior tentorial pits well developed; genal carina pronounced, extending to nearly 0.5× eye height; malar space 0.37× eye height; ratio of lateral ocellus: ocellular distance: postocellar distance as 20:16:42; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 30:9:2:24:21:20:20:19:18:28; funicular segments elongate. Mesosoma: 1.9× as long as broad, pronotum 0.4× as long as broad, mid lobe of mesoscutum 0.85× as long as broad, scutellum about as long as broad; notauli evident as impressed dark lines beneath surface sculpture, axillular grooves evident as rows of foveae; femoral depression nitid, substrigulate on anterior margin; mesepimeron nitid; metapleuron alveolate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a broad, relatively deep, irregularly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina that is laminate distally; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 50:20:11:5:4:6; ratio marginal vein: postmarginal vein: stigmal vein as 19:32:15. Metasoma: Petiole very transverse, gaster 3.6× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:22:22:30:35:20:18:9; hypopygium reaching 0.75× length of gaster, apical region of ventral line with 11 pairs of setae.

*Male*.—Body length 4.7–5.2 mm. Color: as for female, except propodeum some-

times more extensively black and gaster with more dark markings. Scape with whitish oval area opposite insertion of pedicel that protrudes as a prominent knob; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each  $2-3\times$  as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 33:8:2:30:31:31:29:27:25:30. Gastral petiole  $3.2\times$  as long as broad,  $0.95\times$  length of metacoxa, parallel-sided, dorsal surface nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 31:22:15:19:19:18:12:8.

*Diagnosis.*—Like *B. bouceki*, this species has a yellow mesopleuron and scutellum. However, *B. flava* has the top of the head and pronotum black, whereas in *B. bouceki* the body is nearly entirely yellow.

*Variation.*—Female length ranges 5.8–6.2 mm in length.

*Type specimens.*—Holotype, ♀ (USNM): COSTA RICA, Heredia, Puerto Viejo, La Selva, 100 m, i.1991, J. Noyes.

Paratypes, 7♀, 3♂: Limon, 4 km NE Bribri, 50 m, iv–vi.1990, P. Hanson (1♀, MZCR); 7 km SW Bribri, 50 m, ix.1989, P. Hanson (1♂, MZCR); Valle de la Estrella, Reserva Biológica Hitoy Cerere, Sendero Espavel, 240 m, i.2001, F. Umana (1♂, USNM); Sendero Toma de Agua, 100 m, 18.xi–18.xii.2000 (1♂, USNM); 11.x–11.xi.1999 (1♀, USNM); Guanacaste, Estación Pitilla, 9 km S Estación Cecilia, 700 m, 1991 (1♀, USNM); iv.1994, P. Rios (1♀, INBio); Alajuela, San Carlos, Parque Nacional Arenal, Sendero Pilon, 600 m, 9.ix–1.x.1999, G. Carballo (1♀, INBio); Puntarenas, San Luis, Monteverde, 1000–1350 m, viii.1993, Z. Fuentes (1♀, INBio); San Luis, Monteverde, Area de Conservación Arenal, 1000–1350 m, vi.1993, Z. Fuentes, Malaise, L N 449250\_250850, # 2588 (1♀, INBio).

*Etymology.*—From the Latin for yellow, referring to the predominantly yellow coloration of this species.

*Biology.*—Unknown.

*Distribution.*—Costa Rican wet forests, sea level to 1000 m.

*Bephrata leptogaster* Gates and Hanson, **n. sp.**  
(Figs 11, 44, 54)

*Female holotype.*—Body length 6.3 mm. *Color:* head yellow below (except for small black spot in middle of lower face), black above (beginning at toruli), antenna dark brown; mesosoma black except yellow on side of pronotum, fore and middle legs yellow except procoxa partially dark brown, metasomal legs dark brown; metasoma dark brown, yellowish brown ventrally. *Head:*  $1.3\times$  as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, fine, extending  $1/3$  eye height; malar space  $0.27\times$  eye height; ratio of lateral ocellus: ocellular distance: postocellar distance as 15:18:38; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 30:9:2:21:18:21:19:20:18:24. *Mesosoma:*  $2.1\times$  as long as broad, pronotum  $0.7\times$  as long as broad, mid lobe of mesoscutum  $1.2\times$  as long as broad, scutellum  $1.3\times$  as long as broad; notauli as row of foveae and axillular grooves distinctly impressed; femoral depression coriarius; metapleuron foveate; propodeum foveate with a very broad, reticulate median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a rounded lamina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 40:25:12:4:2:6; ratio marginal vein: postmarginal vein: stigmal vein as 21:24:13. *Metasoma:* Petiole very transverse, gaster  $6.9\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:80:30:40:25:5:5:6; Gt1–Gt4 very emarginate medially; hypopygium almost reaching tip of gaster, apical region of ventral line with 10 pairs of setae.

*Male.*—Body length 5.2–6.2 mm. *Color:* as for female, but often with yellow between ocellar area and occiput. Scape without whitish oval area opposite insertion of pedicel; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each  $2-3\times$  as long as



width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 25:7:2:30:35:32:33:30:27:31. Dorsal surface of mesosoma with sculpture unlike that of the female, with strong transverse wrinkles; pronotum shallowly concave. Apex of metatibia with short spur blunt. Gastral petiole  $4.2\times$  as long as broad,  $1.2\times$  length of metacoxa, parallel-sided, dorsal surface nitid; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 26:26:38:30:30:10:13:8.

**Diagnosis.**—This species is quite unlike any other species. The gaster, especially in females, is extremely elongate, about  $6\times$  as long as high. In coloration it is similar to *B. stichogaster*, which also can have a quite elongate gaster, but the wing veins of *B. leptogaster* are very thin, unlike any other *Bephrata*. The males are unlike any other species in having transverse wrinkles on the dorsal surface of the mesosoma, and the dorsal surface of the pronotum is somewhat concave.

**Variation.**—Female length ranges 6.0–6.4 mm in length. Maculation is somewhat variable in extensiveness, but typically not as variable as in species such as *B. cultriformra*.

**Type specimens.**—Holotype, ♀ (USNM): COLOMBIA, with *Cattleya*, v.3.'41, Hoboken 1377, Lot No 41-7524.

Paratypes, 10♀, 5♂, (USNM): same data as holotype (7♀); VENEZUELA, with wild *Cattleya*, 18.v.1945, Hoboken #4300 (1♀); wild *Cattleya*, Wash. D.C. (1♂); among orchid plants, 28.ii.1945, W.W. Chapman (1♂); on window in room with orchids, Hoboken #9360, McMast, 9.iv.1947 (1♂); #9680, Grayson, 13.vi.1947 (2♂); ECUADOR, Orellana, Reserva Etnica Waorani, Transect Ent. 1 km S. Okone Gare Camp, 216.3 m, 00°39'25.7"S 76°27'10.8"W, 4.x.1994, Erwin et al., #859 (1♀, EPNC); PERU, Loreto, Explorama Lodge, 80 km NE Iquitos on Amazon River, 24.vi–20.vii.1990, Menke and Awertschenko (1♀).

**Etymology.**—From the Greek *-leptos* for thin, and *gaster-* referring to the extremely thin gaster.

**Biology.**—Host unknown. Most specimens were collected in association with

orchids, especially *Cattleya* spp. The sculpture of the male is suggestive of parasitoids that emerge from wood.

**Distribution.**—Colombia, Ecuador, Peru, and Venezuela.

*Bephrata lorraineae* Gates and Hanson, n. sp.  
(Figs 12, 43, 56)

**Female holotype.**—Body length 5.8 mm. **Color:** Head yellow except black spot in middle of scrobe, ocellar area, and occiput; antennal pedicel and flagellum dark brown; mesosoma black except pronotum yellow on lateral surface and lateral part of dorsal surface, mesosuctal lobe and lateral part of mid lobe (near notaulix) orange yellow; legs yellow except metatibia black; petiole black; gaster yellow except terga 1 and 7 dark brown, Gt2–Gt6 dark brown dorsally (medially) with posterior band extending ventrally (laterally) on Gt4 and Gt5, Gt3 with ventral band. **Head:**  $1.3\times$  as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present, extending  $0.5\times$  eye height; malar space  $0.30\times$  eye height; ratio of lateral ocellus: ocellocular distance: post-ocellar distance as 20:15:41; antenna with scape reaching middle of anterior ocellus ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 28:8:2:25:23:23:22:20:17:26. **Mesosoma:**  $2.0\times$  as long as broad, pronotum  $0.6\times$  as long as broad, mid lobe of mesoscutum and scutellum each about as long as broad; notauli evident as dark impressed lines beneath surface sculpture, axillular grooves obliterated; femoral depression substrigulate; metapleuron foveate; propodeum foveate-alveolate with a broad, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina that is laminate distally; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 65:30:11:6:4:7; ratio marginal vein: post-marginal vein: stigmal vein as 13:27:8.

**Metasoma:** Petiole very transverse, gaster  $3.6\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 23:21:20:25:36:14:26:5; hypopygium reaching  $0.75\times$  length of gaster, apical region of ventral line with 8 pairs of setae.

**Male.**—Body length 4.6–5.2 mm. **Color:** as for female, except usually with more black on scape, ocellar area (joining with black area in scrobe but not with that in occiput), dorsal surface of pronotum and mesoscutum (lobes remaining at least partially orange yellow in most specimens), and gaster; first metatarsomere frequently darkened, sometimes black. Scape with whitish oval area opposite insertion of pedicel that protrudes as a prominent knob; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each  $2\text{--}3\times$  as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 21:5:2:22:23:22:20:19:17:19. Gastral petiole  $3.5\times$  as long as broad, same length as metacoxa, nearly parallel-sided, dorsal surface mostly nitid (weakly coriaceous in places); ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 35:31:20:22:18:11:14:15.

**Diagnosis.**—This species is most similar to *B. christeri* but has more black on the pronotum; at most, *B. christeri* has just a small black spot at the base of the dorsal surface; in addition the antennal flagellum of the female is uniformly colored whereas in *B. christeri* the last funicular segment and clava are usually darker than the preceding flagellomeres; the male scape of *B. lorrainae* has a protruding apical knob whereas that of *B. christeri* lacks a knob or has a much less protruding knob.

**Variation.**—Female length ranges 3.9–8.3 mm in length and are quite variable in **Color:** the mesoscutal lobes can be either black or orange, and the first metatarsomere is usually light colored but is dark in a few specimens. In many specimens of both sexes, including the holotype, the notauli are distinct (especially when sur-

rounded by orange yellow coloration), but are less distinct in other specimens.

**Type specimens.**—Holotype, ♀ (USNM): COSTA RICA, Puntarenas, R.F. Golfo Dulce, 24 km W Piedras Blancas, 200 m, iv–v.1992, P. Hanson.

Paratypes, 38♀, 7♂: Same data as for holotype (1♀, USNM); ii.1992 (3♀, MZCR); i–iii.1991 (1♀, CNC); iv–v.1991 (2♀, BMNH); vi–vii.1991 (1♀, CNC); xi.1991 (1♀, USNM); xi.1990 (1♂, USNM); 3 km SW Rincón, 10 m, vii.1991, Hanson and Godoy (1♀, MZCR); Peninsula de Osa, Rancho Quemado, 200 m, v.1992, F. Quesada and G. Varela, LS 292500 511000 (1♀, INBio); xii.1992, M. Segura (1♂, USNM); Golfito, Estación Agujas, 300 m, 15.ii–15.iii.2001, J. Azofeifa, LS 526550 276750 (1♀, INBio); 10–20.ii.2001 (1♂, INBio); Cerro Rincón, 645–745 m, 15.iv–15.v.2000, LS 275500 521950 (1♂, MZCR); Parque Nacional Corcovado, Sendero a Río Claro, 0 m, 1991, LS 508300 270500 (1♀, INBio); Limón, 4 km NE Bribri, 50 m, iv–vi.1990, P. Hanson (1♀, MZCR); Sector Cerro Cocori, Finca de E. Rojas, 150 m, vii.1991, E. Rojas, LN 286000 567500 (1♀, INBio); Guanacaste, Estación Pitilla, 9 km S de Sana Cecilia, 700 m, vii.1994, P. Ríos, LN 330200 380200 (1♂, INBio); Estación Murciélagos, 100 m, 28.ix–28.x.1993, E. Araya, LN 320300 347200 (1♀, INBio); Alajuela, Reserva Biológica Alberto Brenes (San Ramón), 900 m, v.2000, P. Hanson (1♀, MZCR). ECUADOR, Orellana, Tiputini, Biodiversity Station, 216 m, 00°37'55"S 76°08'39"W, 7.ii.1999, Lot 2058 Trans 1, T. Erwin et al., Canopy fogging (1♀, USNM); 23.x.1998, Lot 1904 Trans 1 (1♀, USNM); Lot 1901 (1♀, USNM); 9.ii.1999, Lot 2003 Trans 1 (1♀, USNM); nr Yasuni National Park, 220–250 m, T6/Sta.8, 1.vii.1998, Lot 1857 (1♀, USNM); Napo, Reserva Etnica Waorani, Trans Ent. 1 km S. Okone Gare Camp, 00°39'10"S 76°26'0", 220 m, 20.vi.1994, T. Erwin et al., Canopy fogging, Lot 688 (1♂, USNM); 6.x.1994, Lot 880 (1♀, USNM); 2.vii.1995, Lot 1063 (1♀, USNM); Lot 1090 (1♀, USNM); Lot 1093 (1♀, USNM); 9.x.1999, Lot 1257 (1♀, USNM); 5.x.2000, Lot 1755 (1♀, USNM); 00°39'25.7"S 76°27'10.8", 216.3 m, 4.x.1996, Lot 1753 (1♀, USNM); Chimborazo, Narnajapata, Chilicay, 16.vi.1955, R. LeviCastillo (1♀, USNM). PERU, Loreto, Camp. S. Branch, 75.20W 05.12E, Igapo Forest, 12.v.1990, T. Erwin, Fogging (1♀, 1♂, USNM); Explomapo, Camp. Río Napo, Río Sucusari, 100 m, 15.vi.1996, 03°15'S 072°55'W, Lot 382, T. Erwin (1♀, USNM); COLOMBIA,



Amazonas, Productividad Primaria Neta Amacayacu, San Martin, 150 m, 3°23'01"N 70°06'01"W, 22–30.v.2000, B. Amado #90 (1♀, USNM); Bolivar SFF, Los Colorados, La Suiris, 9°54'00"N 75°07'00"W, 126 m, 1–15.ix.2000, E. Deuluteut, 617 (1♀, USNM); VENEZUELA, Caracas, with *Cattleya* sp., San Francisco, #20585, 29.iii.1946 (1♀, USNM); UNKNOWN, window sill inspection room, Hoboken, N.J., 29.vii.1949, F. Perlmutter (1♀, USNM); Miami, Fla. Port, 29.iv.1969, U.C.Buff (1♀, USNM); Miami, Florida Inspection House, 15.vii.1969, F. Matthews (1♀, USNM).

*Etymology*.—Named in honor of Lorraine, the daughter of the second author.

*Biology*.—Host unknown. A specimen from Venezuela was associated with *Cattleya* orchids.

*Distribution*.—Costa Rica (0–900 m), Colombia, Ecuador, Peru, and Venezuela.

*Bephrata nigracephala* Gates and Hanson, **n. sp.**  
(Fig. 13)

*Female holotype*.—Body length 3.9 mm. *Color*: black except yellow on scape, pronotum, fore and middle legs, metatarsus, and large areas on basal 1/2 of gaster; antennal pedicel and flagellum dark brown. *Head*: 1.3× as broad as high; clypeus with apical margin straight, curved slightly inward; anterior tentorial pits difficult to discern (due to black coloration of lower face); genal carina present, extending 0.5× eye height; malar space 0.44× eye height; ratio of lateral ocellus: ocellocular distance: postocellar distance as 16:13:38; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 22:7:2:21:16:16: 16:14:14:17. *Mesosoma*: 2.1× as long as broad, pronotum 0.8× as long as broad, mid lobe of mesoscutum and scutellum about as long as broad; notauli as a row of foveae and axillular grooves obliterated; femoral depression substrigulate; metapleuron foveate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a narrow medial groove anteriorly (disappearing posterior-

ly); basal anterior portion of procoxa with large oblique depression, bordered mesally by a carinate ridge that forms a semicircle (convex side directed laterally); apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 75:26:13:9: 5:10; ratio marginal vein: postmarginal vein: stigmal vein as 30:41:17. *Metasoma*: Petiole about 4× as long as broad (about as long as metacoxa), parallel-sided but widened at base, then narrowed and widened again; gaster 2.4× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 17:15:14:19:13:15:7:5; hypopygium reaching 0.7× length of gaster, apical region of ventral line with 5 pairs of setae.

*Male*.—Unknown.

*Diagnosis*.—This species and *B. petiolata* are the only species in the genus where the female has an elongate petiole, but *B. nigracephala* is readily distinguished by its completely black head, a characteristic that is unique among species of *Bephrata*.

*Variation*.—Known from one female.

*Type specimens*.—Holotype, ♀ (USNM): ECUADOR, Orellana, Tiputini Biodiv. Station, nr N.P. Yasuni, 8.ii.1999, 220–250 m, Trans 4, Sta. 5, 00°37'55"S 76°08'39"W, T. Erwin et al., #2034, fog terre firme forest.

*Etymology*.—From the Latin for black and Greek for head, referring to the completely black head of this species.

*Biology*.—Unknown.

*Distribution*.—Amazon basin of Ecuador.

*Bephrata noyesi* Gates and Hanson, **n. sp.**  
(Fig. 14)

*Female holotype*.—Body length 4.0 mm. *Color*: Head orange yellow below, black above toruli; antennal scape yellow, flagellum dark brown; mesosoma black except yellow on pronotum; fore and middle legs orange yellow, metacoxa and tarsus pale yellow, femur and tibia largely dark brown; petiole black; gaster yellow except terga 1 and 6–7 dark brown, Gt3–Gt4 dark brown dorsally (medially) with posterior band extending ventrally (laterally), Gt5

with narrow brown band posteriorly. Head:  $1.3\times$  as broad as high; clypeus with apical margin straight, curved slightly inward; anterior tentorial pits small; genal carina present but fine, extending  $1/3$  eye height; malar space  $0.26\times$  eye height; ratio of lateral ocellus: ocellocular distance: postocellar distance as 20:10:31; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 28:9:2:20:19:19:17:14:17. Mesosoma:  $1.85\times$  as long as broad, pronotum  $0.7\times$  as long as broad, mid lobe of mesoscutum  $0.9\times$  as long as broad, scutellum about as long as broad; notauli as a row of foveae and axillular grooves obliterated; femoral depression substrigulate; metapleuron foveate; propodeum alveolate (with numerous carinae forming irregular setose cavities), without an evident longitudinal groove in center, except at base; basal anterior portion of procoxa with large oblique depression, bordered mesally by a carinate ridge that forms a semicircle (convex side directed laterally); apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 41:14:8:6:4:6; ratio marginal vein: postmarginal vein: stigmal vein as 23:34:14. Metasoma: Petiole about as long as wide, gaster  $2.9\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 18:9:15:21:22:30:2:4; hypopygium reaching  $0.6\times$  length of gaster, apical region of ventral line with 5 pairs of setae.

Male.—Body length 3.2–3.4 mm. Color: as for female, except dorsal surface of pronotum partially to nearly completely black. Scape with very minute whitish oval area at apex; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each  $2\text{--}3\times$  as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 31:6:2:32:32:30:26:26:22:25. Gastral petiole  $2.8\times$  as long as broad,  $0.8\times$  length of metacoxa, nearly parallel-sided, dorsal surface coriaceous; ratio of petiole:

Gt1–Gt7 (dorsal length measured in lateral view) as 18:30:16:10:9:10:1:4.

Diagnosis.—This is the only species of *Bephrata* in which the female petiole is quadrate. The male is quite similar to those of *B. christeri* and *B. lorraineae*, but can be distinguished from the latter by the absence of an apical knob on the scape, and from the former by the slightly shorter, reticulate petiole.

Variation.—Female length ranges 3.8–5.3 mm in length. Two of the three specimens from Ecuador (Tiputini Biodiversity Station) are either variants of this species or a new species. Both are females and the last two flagellomeres are darker than the preceding ones, the vertex is less black (restricted to the ocellar region instead of being all black), and the pronotum has a black spot in the middle (instead of being almost entirely yellow).

Type specimens.—Holotype, ♀ (USNM): COLOMBIA, Amazonas, 150 m, Parque Nacional Natural Amacayacu Matamata, San Martin,  $3^{\circ}23'01''\text{N } 70^{\circ}06'01''\text{W}$ , 2–10.x.2000, B. Armando, M.843.

Paratypes, 9♀, 4♂: same data as for holotype except 10–18.x. 2000, M.835 (2♀, USNM); 19–26.iii.2000, M.82 (1♂, IAVH); 300 m, 19–28.iii.2000, A. Parente #99 (1♂, USNM); 6–15.iv.2000, M84 (1♀, IAVH); 24.iv–5.v.2000, M88 (1♂, USNM); 2–8.v.2000, #682 (1♀, USNM); 8–14.viii.2000, #689 (1♀, IAVH); 15–23.x.2000, #849 (1♀, USNM). ECUADOR, Napo, Tiputini, Biodiversity Station, 216 m,  $00^{\circ}37'55''\text{S } 76^{\circ}08'39''\text{W}$ , 23.x.1999, Lot 1914 Transect 2, T. Erwin et al., Canopy fogging (1♀, USNM); 6.ii.1999, Lot 2068 Tans 7 (1♀, USNM); 220–250 m T8/Sta.4, 4.vii.1998, Lot 1873 (1♀, USNM); PERU, Loreto, 1 km SW Boca del Rio Samiria, Vigilante Post #1, 31.viii.1991,  $04^{\circ}40'29''\text{S } 74^{\circ}18'54''\text{W}$ , T. Erwin fogging, 130 m, Lot 74 (1♂, USNM).

Etymology.—Named in honor of John Noyes, for his contributions to our knowledge of Neotropical Chalcidoidea.

Biology.—Unknown.

Distribution.—Upper Amazon basin of Colombia, Ecuador, and Peru.



*Bephrata nublada* Gates and Hanson, **n. sp.**  
(Figs 15, 53)

*Female holotype*.—Body length 5.2 mm. Color: Black/dark brown: flagellum, occiput, lateral lobe of mesoscutum in medial 1/2, mesoscutum, medial 3/4 axilla, scutellum, propodeum, mesepimeron, metapleuron, metatibia except tips, Gt<sub>1</sub>, Gt<sub>4</sub>, apical 2/3 Gt<sub>5</sub>, apical 2/3 syntergum, ovipositor sheaths, midline of hypopygium; orange: scape, pedicel, pronotum, prepectus, tegula, mesepisternum, lateral 1/2 lateral lobe of mesoscutum, lateral 1/4 axilla, legs; pale yellow: coxae, remainder of gaster, Fore wings hyaline with infusate cloud in disc posterad stigmal vein. Head: 1.3× as broad as high; clypeus with apical margin straight, with notch on each side, anterior tentorial situated in notch; genal carina present, extending 0.5× eye height; malar space 0.5× eye height; ratio lateral ocellus:ocellular distance:postocellar distance as 10:6:25; scape reaching just above anterior ocellus; ratio scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 42:11:3:24:18:17:17:15:14:48 (Fig. 15). Mesosoma: 2.8× as long as broad, pronotum 0.5× as long as broad, mid lobe of mesoscutum about as long as broad, scutellum about as long broad; notauli obliterated posteriorly, barely evident anteriorly; axillular grooves obliterated; scutellum with foveae very shallow and sparse (interstices broad); femoral depression weakly coriarius-substrigulate, adscrobal carina weak, ventral-posterior epicnemium with relatively few foveae; metapleuron alveolate; propodeum with numerous carinae forming irregular setose cavities, median channel shallow, widest medially, with irregular longitudinal striae; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 103:43:22:13:8:19; ratio marginal vein:postmarginal vein:stigmal vein as 35:67:31. Metasoma: Petiole with

dorsal length 0.3× as long as broad, produced anterolaterally into dull prongs; gaster about 3.6× as long as high; ratio of Gt<sub>1</sub>–Gt<sub>7</sub>, ovipositor sheath (all measured dorsally): 20:34:60:73:32:48:19; hypopygium reaching about 0.75× length of gaster, apical region of ventral line with 9 pairs of setae.

*Male*.—Body length 4.6 to 5.3 mm. Color: dark areas of gaster described for female more extensive dorsally. Sculpture as for female, except prodeum medially with more longitudinal rugosity and fine carinae. Scape with light colored oval area opposite insertion of pedicel, this area protruding as a knob; flagellomeres pedicellate with a basal and an apical whorl of erect setae each 3–4× as long as width of segment; ratio scape (minus radicle): pedicel: anellus: F1–F6: clava as 40:8:3:34: 34:34:34:30:26:32. Gastral petiole 3.1× as long as broad, 0.7× as long as metacoxa; parallel-sided, dorsal surface weakly coriarius especially on basal 1/2; ratio of petiole: Gt<sub>1</sub>–Gt<sub>7</sub> (dorsal length measured in lateral view) as 27:28:18:18:18:6: 11:10

*Diagnosis*.—*Bephrata nublada* is the only species known having an infusate spot on the fore wing.

*Variation*.—Female length ranges 5.2–5.4 mm. There is little color variation in the type material.

*Type specimens*.—Holotype, ♀ (USNM): COSTA RICA, Prov. Limón, Parque Internacional La Amistad, Valle del Silencio, Zona de Acampar, 2450 m, 18.iv.2001, J. Azofiefa, Trampa de Luz, L\_S\_341250\_577200, #63242.

Paratypes, 1♀, 5♂: same data as for holotype (2♂, MZCR, USNM); COSTA RICA, Puntarenas, Bahía Wafer, Isla del Coco, 1 m, vii.2001, Y. Camacho, Malaise, Long\_-87:03:30.0000 Lat\_5: 32:45.0000 #3243 (1♀, 2♂, INBio); Bahía Chatan, Isla del Coco, 5–9.ii.1993, L-S 0,0, INBio CRI001851156 (1♂, INBio).

*Etymology*.—This species is named for the cloudy infuscation in the fore wing.

*Biology*.—Host unknown.

*Distribution*.—Costa Rica.

*Bephrata petiolata* Gates and Hanson, n. sp.  
(Figs 16, 55)

*Female holotype*.—Body length 4.0 mm. *Color*: Head yellow below, black above anterior ocellus; scape yellow, rest of antenna orange yellow except last funicular segment and clava which are dark brown; mesosoma black except yellow pronotum (small black spot in middle); legs yellow except for black metatibia; petiole black; gaster yellow except terga 1 and 6–7 dark brown, Gt2–Gt5 dark brown dorsally (medially) with posterior band extending ventrally (laterally). *Head*:  $1.3\times$  as broad as high; clypeus with apical margin straight, curved slightly inward; anterior tentorial pits small; genal carina present, extending  $0.5\times$  eye height; malar space  $0.4\times$  eye height; ratio of lateral ocellus: ocellocular distance: postocellar distance as 17:12:30; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 23:7:2:21:16: 15:15:14:11:14. *Mesosoma*:  $2.1\times$  as long as broad, pronotum  $0.7\times$  as long as broad, mid lobe of mesoscutum  $0.7\times$  as long as broad, scutellum about as long as broad; notauli as a row of foveae and axillular grooves obliterated; femoral depression substrigulate; metapleuron foveate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a faint, narrow, longitudinal groove in center; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carinate ridge that is laminate distally; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 75:28:15:9:4:10; ratio marginal vein: postmarginal vein: stigmal vein as 6:10:4. *Metasoma*: Petiole about  $5\times$  as long as wide (about as long as metacoxa), parallel-sided but widened at base, then narrowed and widened again; gaster  $2.4\times$  as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 21:11:13:16: 11:16:6:6; hypopygium reaching  $0.7\times$

length of gaster, apical region of ventral line with 6 pairs of setae.

*Male*.—Unknown

*Diagnosis*.—This species and *B. nigracephala* are the only species of *Bephrata* where the female has an elongate petiole, but *B. petiolata* is readily distinguished by its yellow face (as opposed to black in *B. nigracephala*).

*Variation*.—Female length ranges 3.6–4.1 mm in length. The size of the black spot on the pronotum and the degree of contrast in the colors of the antennal flagellum vary somewhat.

*Type specimens*.—Holotype, ♀ (EPNC): ECUADOR, Orellana, Tiputini, Biodiversity Station, 216 m,  $00^{\circ}37'55''\text{S}$   $76^{\circ}08'39''\text{W}$ , 23.x.1998, Lot 1901 Trans 1, T. Erwin et al., Canopy fogging bare leaves, some w/ bryophytic/lichenous coat.

Paratypes, 3♀: same data as for holotype except Lot 1916, Trans 3 (1♀, EPNC); 220–250 m, 1.vii.1998, Trans 6, Sta.1, #1850 (1♀, USNM); Napo, Reserva Ethnica Waorani, Transect Ent., 1 km S. Okone Gare camp,  $00^{\circ}39'10''\text{S}$   $76^{\circ}26'0''$ , 220 m, 2.vii.1995, Lot #1090 (1♀, USNM).

*Etymology*.—Named for the elongate petiole of this species.

*Biology*.—Unknown.

*Distribution*.—Amazon basin of Ecuador.

*Bephrata ruficollis* Cameron  
(Figs 17, 28–30, 32–39, 46)

*Bephrata ruficollis* Cameron 1884: 109. Lectotype ♀, designated below. Panama, V. de Chiriqui (BMNH).

*Female lectotype*.—Body length 6.8 mm. *Color*: Orange except following areas black: vertex transversely encompassing posterior ocelli, mesoscutum, scutellum, dorsellum, propodeum, petiole, gastral terga dorsally; or dusky: apical three flagellomeres. *Head*:  $1.3\times$  as broad as high; clypeus with apical margin minutely emarginate; anterior tentorial pits small; genal carina present but short, extending to venter of eye (Fig. 34); malar space  $0.4\times$  eye height (Fig. 33); ratio lateral ocellus: ocellocular distance: postocellar distance as



14:24:6; scape reaching just to anterior ocellus; ratio scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:F6: club as 40:10:2:35:26:30:20:15:14:31 (Fig. 37). Mesosoma: 2.3× as long as broad, pronotum 0.5× as long as broad, mid lobe of mesoscutum 1.3× as long as broad, scutellum 1.3× as long as broad; notauli mostly obliterated (evident only as shallow impressions), axillular grooves evident as rows of foveae; femoral depression substrigulate, ventral-posterior epicnemium with relatively few foveae; metapleuron alveolate; propodeum with numerous carinae forming irregular setose cavities, median channel broad, rugulose with a few cross carinae forming asetose cells; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 150:45:25:12:8:19; ratio marginal vein: postmarginal vein: stigmal vein as 70:105:48 (Fig. 38). Metasoma: Petiole 0.2× as long as broad, unproduced anterolaterally (Fig. 32); gaster about 3× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 40:70:45:65:80:40:20:10; [hypopygium nearly reaching 0.9× length of gaster, apical region of ventral line with 15–18 pairs of setae].

Male.—Body length 4.1 to 6.2 mm. Color: Black areas of gaster described for female more extensive dorsally; antenna entirely black except tip of clava whitish. Scape with light colored ventral plaque in apical 1/3, not protruding as knob; flagellomeres elongate and of uniform width (Fig. 46), the shortest 5.6× as long as broad, evenly covered with suberect setae each ~1.0× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1–F6: clava as 45:10:3:58:55:55:50:48:46:45 (Fig. 46). Gastral petiole 2.7× as long as broad, subequal in length to metacoxa, nearly parallel-sided but broadest medially, dorsal surface weakly coriaceous to nitid; ratio of petiole: Gt1–Gt7

(dorsal length measured in lateral view) as 32:30:23:25:15:18:12:15.

Diagnosis.—*Bephrata ruficollis* has the metatibia completely yellow and is the only species in which the clava is white, differing from the other brown/black flagellomeres.

Variation.—Female length ranges 5.0–7.0 mm. Some females have more extensive maculation encompassing the occiput along with reduced dorsal maculation on the gaster, particularly anteriorly. The median channel in the aforementioned specimens possess smoother sculpture. One male has a circular black maculation dorsomedially on the pronotum.

Type specimens.—Lectotype ♀, here designated (BMNH): V. de Chiriqui, 3–4,000 ft., Champion, P. Cameron coll. 1914–110, B.M. Type Hym. 5.313 (Panama).

Other specimens examined.—COSTA RICA: Guanacaste, Estación Pitilla, 9 km S. Santa Cecilia, 700 m, ix.1988, I. Gauld (3♂, MZCR); Heredia, F. La Selva, 3 km S. Puerto Viejo, 10°26'N 84°01'W, 3.vii.1986, dead trees, H. A. Hespenheide (1♀, USNM); F. La Selva, 3 km S. Puerto Viejo, 10°26'N 84°01'W, 1.iv.1980, H. A. Hespenheide (1♀, USNM); La Selva Biological Station, 3 km S. Puerto Viejo, 10°26'N 84°01'W, 23.iv.1989, H. A. Hespenheide (1♀, USNM); Estación Biológica La Selva, 50–150 m, 10°26'N 84°01'W, Proy. ALAS, INBio -OET, M/05/352, 15.ii.1994, bosque primerio (1♀, INBio); Puerto Viejo, La Selva, 100 m, i–ii.1991, P. Hanson (2♀, MZCR); Chilamate, 75 m, vii–viii.1989, P. Hanson (3♀, MZCR); same locality as preceding but dates as: xii.1989–iii.1990 (2♀, 2♂, USNM); ix–x.1989 (2♀, 2♂, MZCR); vii–x.1990 (1♂, MZCR); Reserva Biológica Carara, Estación Quebrada Bonita, 50 m, v–vi.1989, P. Hanson (1♂, USNM); Golfo Dulce, 24 km W. Piedras Blancas, 200 m, ix–xi.1989, Hanson (1♂, USNM); same locality but dates as: vi–viii.1989 (1♂, USNM); San Vito, Jardín Botánico Las Cruces, vii–viii.1988, 1200 m, P. Hanson (2♀, 3♂, USNM); same locality but dates as: viii–ix.1988 (2♀, USNM); 5.vi.1988 (1♀, USNM); vi–vii.1988 (1♀, 1♂, USNM); xii.1988 (2♀, USNM); Golfito, Parque Nacional Corcovado, Sendero a Sirena, 100 m, 15.vi–15.vii.2000, L\_S\_514200\_276500, J. Azofiefa, Malaise, # 57968 (1♀, USNM); San José,

Ciudad Colón, 800 m, ii.1990, L. Fournier (1♂, MZCR); same locality but dates as: iv–v.1990 (2♀, MZCR); xii.1989 (1♀, MZCR). ECUADOR, Napo, Tiputini Biodiversity Station, 216 m, 5.ii.1999, 00°37'55"S 76°08'39"W, Lot 2096, Transect 10, T. Erwin et al., canopy fogging bare leaves, some with bryophytic/lichenous coat (1♀, USNM); Reserva Etnica Waorani, Transect Ent. 1 km S. Okone Gare Camp, 220 m, 00°39'25.7"S, 76°27'10.8"W, 7.ii.1996, T. Erwin et al., #1443, t5.3, terre firme forest (1♂, EPNC). VENEZUELA, San Esteban, xi.1939, Pablo Anduze (2♀, USNM).

*Biology*.—Host unknown.

*Distribution*.—Costa Rica, Ecuador, Panama, and Venezuela.

*Bephrata stichogaster* Gates and Hanson, **n. sp.**  
(Fig. 18)

*Female holotype*.—Body length 5.6 mm. Color: Head yellow except black spot below eye, area from scrobe to ocelli, and occiput; clava darker than rest of antenna; mesosoma black except yellow on lateral surface of pronotum; legs yellow except metatibia black; petiole black; gaster with terga 1, 6 and 7 dark brown, Gt2–Gt5 dark brown dorsally (medially) with broad, longitudinal, pale band laterally followed by dark band below. Head: 1.3× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present but weak, extending 0.5× eye height; malar space 0.4× eye height; without evident line between anterior ocellus and scrobal basin; ratio of lateral ocellus: ocellocular distance: postocellar distance as 19:15:36; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 26:9:2:19:17:17:17:16:14:19. Mesosoma: 1.9× as long as broad, pronotum 0.7× as long as broad, mid lobe of mesoscutum and scutellum, each about as long as broad; notauli and axillular grooves mostly obliterated; femoral depression substrigulate-coriarius; metapleuron alveolate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a broad, relative-

ly deep, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina that is laminate distally; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 85:32:15:9:5:12; ratio marginal vein: postmarginal vein: stigmal vein as 17:25:11. Metasoma: Petiole very transverse, produced laterally as upturned spurs; gaster 4.7× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 35:28:24:27:34:15:14:8; hypopygium reaching 0.8× length of gaster, apical region of ventral line with 8 pairs of setae.

*Male*.—Body length 4.2–5.2 mm. Color: as for female, except head sometimes completely black from scrobe to occiput, gaster often darker with pale lateral stripe less evident, and metatarsi sometimes dark. Scape with whitish oval area opposite insertion of pedicel, but not protruding as a knob; flagellar segments elongate and of uniform width, evenly covered with sparse suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 20:5:2:19:19:18:17:15:13:15. Gastral petiole 3.9× as long as broad, 1.1× length of metacoxa, parallel-sided, dorsal surface mostly nitid, weakly coriarius at base; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 35:26:20:19:20:18:13:10.

*Diagnosis*.—This species is most similar to *B. leptogaster* in that both species have a very narrow, elongate gaster; however, the fore wing veins of *B. leptogaster* are very thin, whereas the veins of *B. stichogaster* are more like those of other *Bephrata*; the males of *B. leptogaster* have transverse wrinkles on the mesoscutum and scutellum, whereas the sculpture of *B. stichogaster* is more like that of other *Bephrata* (foveate). Females are readily distinguished from other *Bephrata* by the longitudinal, pale stripe on the side of the gaster. However, this stripe is often less evident in males, making them more difficult to distinguish from other *Bephrata*, especially *B. christeri* which also



lacks a protruding knob on the apex of the scape and has a shiny petiole; the latter species usually has the mesoscutal lobes orange (reddish) yellow, whereas in *B. stichogaster* the entire mesoscutum is black.

**Variation.**—Female length ranges 4.6–6.6 mm in length. Some specimens of both sexes have the top of the head completely black, as opposed to having at least some yellow between the ocellar area and the occiput; the dorsal pronotum varies from nearly all black (sides yellow) to entirely black. Some specimens, especially in males, have the metacoxa black and sometimes also a black spot the metafemur. The male flagellum is usually yellowish brown but in a few individuals it is black.

**Type specimens.**—Holotype, ♀ (USNM): COSTA RICA, Heredia, Estación Biológica La Selva, 100 m, 10°26'N 84°01'W, 14.x.1994, FPM 23.

Paratypes, 15♀, 15♂: same data as for holotype except 23.vi.1985, H. A. Hespeneide (1♀, USNM); Alajuela, 5 km W San Ramon, 1200 m, x.1996, O. Castro and P. Hanson (1♀, MZCR); vi.1997 (1♀, MZCR); vii.1997 (1♀, USNM); Guanacaste, Bara Honda, 200 m, v.1988, Gauld and Mitchell (2♀, MZCR); Rio San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, xi.1992, G. Rodriguez, LN 287800 427600 (1♀, INBio); Z. P. Nasara, Sendero La Ceiba, 600 m, 16.viii–21.ix.2001, I. Jimenez, LN 221100 382950 (1♂, INBio); San Jose, Zurqui de Moravia, 1600 m, vii.1991, P. Hanson (1♂, MZCR); Rio Sur, 160 m, Reserva Biológica Carara, ii–iii.1990, LN 194300 478250 (1♂, INBio); Puntarenas, San Luis, Monteverde, 1000–1350 m, ii.1995, Z. Fuentes, LN 250850 449250 (1♂, INBio); Reserva Natural Cabo Blanco, Estación San Miguel, ix.1993, M. Ramirez, LS 173174 411412 (1♀, BMNH); Buenos Aires, Parque Internacional La Amistad, Estación Altamira, Cerro Quemado, 2279 m, 13.xi–13.xii.2001, D. Rubi, LS 336200 575560 #66667 (2♂, INBio). COLOMBIA, orchid, in cargo, 8.viii.1940, Hoboken, #239 (2♂, USNM); 6.viii.1940, #224 (1♂, USNM). MEXICO, Veracruz, Estación Biológica Los Tuxlas 18°35'N 95°05'W, 25.iv.1991, H. A. Hespeneide (1♀, USNM); ca. 15 km N of Catemaco, 15–17.ix.1987, A. L. Norrbom (1♀, USNM); 33 km NE Catemaco, 160 m, 1.vii.1983, M. Kaulbars

(1♂, USNM); Martinez de la Torres, with *Philodendron* cane, Randolph, 24.ix.1947, Laredo, Texas, No. 44943 (1♂, USNM); V.C., Laredo port of entry, 1.v.1962, orchid (1♂, USNM); San Luis Potosi, with orchid plants from Tamazunchela, Laredo, Tx., No. 46983, Lewis, 31.vii.1948 (1♂, USNM); in pseudobulb of *Laelia* sp. from Mexico, Brownsville #66607, at airport, 22.vii.1948 (2♀, USNM); with orchid plants from Mexico, Randolph, 22.ix.1947, Laredo, No. 44901 (1♀, USNM); orchid plants, Mexico, Brownsville, Texas 75661, 13.iv.1954, 4094 (1♂, USNM); Laredo POE, 23.v.1955, on orchid, Watt (1♀, USNM). PANAMA, Canal Zone, Barro Colorado Island, 9°10'N 79°50'W, 20.vi.1977, H. A. Hespeneide (1♂, USNM). TRINIDAD AND TOBAGO, Tunapuna, Mt. St. Benedict, 500 m, 21.vi–8.vii.1993, Tapor rain forest MT, S. and J. Peck (1♂, CNC). UNKNOWN, Miami, Fla., Port, on window, 17.viii.1965, L. A. McClain (1♀, USNM). VENEZUELA, with wild orchids, Hoboken, #252, 13.viii.1940 (1♀, USNM).

**Etymology.**—From the Greek *stichos* for line, referring to the pale longitudinal line on the side of the gaster,

**Biology.**—Host unknown. Many specimens were collected at port-of-entries associated with orchids, two of them “in pseudobulbs of *Laelia* sp.” from Mexico. Another Mexican specimen was collected in association with *Philodendron* (Araceae) “canes”.

**Distribution.**—Colombia, Costa Rica, Mexico (Veracruz, San Luis Potosí), Panama, Trinidad and Tobago, and Venezuela. In Costa Rica, this species occurs in both wet and seasonally dry forests from sea level to 1200 m, although there is one male from 1600 m which has somewhat aberrant coloration (e.g., the flagellum completely black).

*Bephrata ticos* Gates and Hanson, n. sp.  
(Fig. 19)

**Female holotype.**—Body length 6.0 mm. **Color:** Head yellow except black from scrobe to back of head and a small spot below eye; antennal flagellum dark brown; pronotum mostly black dorsally and yellow laterally; mesoscutum and scutellum orange (reddish) yellow except for thin black line in middle and broad band at

anterior end of mid lobe; mesopleuron, metapleuron, and propodeum black; legs yellow except metatibia black; petiole black; gaster yellow except terga 1 and 7 dark brown, Gt2–Gt6 dark brown dorsally (medially), Gt3–Gt5 with posterior band extending ventrally (laterally). Head: 1.4× as broad as high; clypeus with apical margin straight; anterior tentorial pits small; genal carina present but weak, extending about 1/4 eye height; malar space 0.35× eye height; ratio of lateral ocellus: ocellular distance: postocellar distance as 22:19:44; antenna with scape reaching middle of anterior ocellus; ratio of scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 20:6:2:18:16:16:16:15:14:19. Mesosoma: 1.9× as long as broad, pronotum 0.5× as long as broad, mid lobe of mesoscutum and scutellum each about as long as broad; notauli and axillular grooves evident as weak lines beneath surface sculpture; femoral depression substrigulate, more strongly sculptured on anterior margin; metapleuron alveolate; propodeum alveolate (with numerous carinae forming irregular setose cavities), with a broad, shallow, weakly sculptured median channel; basal anterior portion of procoxa with large oblique depression, bordered mesally by a sinuous carina that is laminate distally; apex of metatibia with a short pointed spur; ratio metatibia: metatarsomeres as 50:22:10:5:3:8; ratio marginal vein: postmarginal vein: stigmal vein as 16:22:11. Metasoma: Petiole very transverse, produced laterally as upturned spurs; gaster 3.4× as long as high; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:22:15:35:35:22:15:9; hypopygium reaching 0.75× length of gaster, apical region of ventral line with 10 pairs of setae.

Male.—Body length 4.2–4.7 mm. Color: as for female, except gaster darker. Scape with whitish oval area opposite insertion of pedicel that protrudes as a prominent knob; flagellar segments elongate and of uniform width, evenly covered with sparse

suberect setae, each 2–3× as long as width of corresponding segment; ratio scape (minus radicle): pedicel: anellus: F1: F2: F3: F4: F5: F6: clava as 20:4:1:19:20:20:19:15:13:15. Gastral petiole 3.9× as long as broad, same length of metacoxa, parallel-sided, dorsal surface mostly nitid, weakly coriarius at base; ratio of petiole: Gt1–Gt7 (dorsal length measured in lateral view) as 35:31:22:22:20:12:16:14.

Diagnosis.—The combination of an orange (reddish) yellow mesoscutum and scutellum, with a black mesopleuron and propodeum is unique; only *B. bahiae* has a similar color pattern, but in this latter species the mesoscutum and scutellum are pale yellow, and there is less black on the head and pronotum.

Variation.—Female length ranges 5.7–6.1 mm in length and show relatively little variation in color, principally whether or not there is a thin, black medial line present on the mesoscutum and scutellum.

Type specimens.—Holotype, ♀, (USNM): COSTA RICA, Puntarenas, San Vito, Estación Biológica Las Alturas, 1500 m, vii–viii.1991, P. Hanson.

Paratypes, 32♀, 10♂: same data as holotype (1♀, 1♂, MZCR); xi.1991 (1♀, MZCR); iii.1992 (2♀, 2♂, MZCR); v.1992 (4♀, 2♂, USNM); vi.1992 (3♀, BMNH); xi–xii.1992 (1♀, CNC); iii.1993 (1♀, CNC); iv.1993 (1♂, BMNH); iii.1992, M. Ramirez, LS 322500 591300 (1♀, INBio); viii.1992, M. Ramirez and E. Sancho (3♀, INBio); 3–4.ix.1992, E. Sancho (1♂, INBio); Buenos Aires, Parque Internacional La Amistad, Sendero Gigantes, 1460 m, 9.viii–9.ix.2001, D. Rubí, LS 331800 572100 (7♀, INBio); 9.vii–9.viii.2001 (1♀, INBio); 10.vi–10.vii.2001 (1♂, INBio); Estación Altamira, 1320 m, x.1994, M. Segura and Z. Fuentes, LS 331700 572100 (1♀, INBio); Area de Conservacion Amistad, Sector Altamira, 1 km S.O. del Cerro Billey, 1400 m, x.1994, M. Segura, LS 331500 571700 (1♀, INBio); Parque Internacional La Amistad, 1400 m, viii.1994, R. Delgado, LS 332700 572400 (1♀, INBio); Parque Internacional La Amistad, Finca Cafrosa, 1100 m, iv–x.1989 (2♀, 1♂, MZCR); RF Golfo Dulce, 3 km SW Rincón, 10 m, xii.1992, Hanson and Godoy (1♀, USNM); Parque Nacional



Corcovado, Estación Sirena, 0–100 m, 9–27.vii.1992, A. Gutierrez, LS 270500 508300 (1♂, USNM); San José, Zurquí de Moravia, 1600 m, v.1996, Hanson and Godoy (1♀, USNM).

**Etymology.**—Noun in apposition named for the local slang term, “ticos”, used to denote inhabitants of Costa Rica.

**Biology.**—Host unknown.

**Distribution.**—*Bephrata ticos* is presently known only from Costa Rica; the vast majority of specimens (42) are from montane sites (1100–1600 m), primarily the Talamanca Mountains, although there are two from lowland sites (Osa Peninsula).

### *Isosomodes* Ashmead

*Isosomodes* Ashmead 1888: 42, 43. Type species:

*Isosoma gigantea* Ashmead, by subsequent monotypy.

**Description (females).**—Length 3.5–7.5 mm. **Color:** Usually a combination of yellow, orange, and black, sometimes completely dark brown/black; middle terga of gaster often with black band along posterior margin (appearing like vertical tiger stripes), becoming weaker ventrally (Figs. 20–27). **Sculpture:** head (except gena), dorsal mesosoma, lateral and posterior part of epicnemium, metapleuron, and lateral areas of propodeum covered with setigerous foveae (‘umbilicate punctures’), interstices appearing microreticulate at low magnification (Fig. 72); supraclypeal area usually without striae converging on clypeus (Fig. 68), occasionally few fine striae present, gena and lateral panel of pronotum weakly sculptured, imbricate to reticulate with occasional fovea; prepectus weakly sculptured, shallowly concave along dorsoventral axis; femoral depression coriarius, foveolate and/or substrigulate, mesepimeron substrigulate to foveolate, sometimes smooth (Figs. 72, 75); metepimeron and lateral areas of propodeum deeply foveate; coxae weakly sculptured, usually imbricate to reticulate; metatibia appearing longitudinally rugose from presence of raised, elongate carinae; metasoma nitid, often finely imbricate

posteriorly (Fig. 67). **Head:** slightly wider than high in frontal view; mandible with two pointed teeth ventrally and a truncate tooth dorsally; anterior clypeal margin straight and/or notched (Fig. 68); torus situated above middle of eye and antennal scape often extending above vertex; intertorular space narrow, with a semicircular plate/carina extending to base of scape, continuing as raised lineation to near middle of scrobal basin but becoming very weak and often difficult to discern dorsally; scrobal basin very weakly sculptured, carinate laterally; anterior ocellus situated adjacent to scrobal basin, separated by at most foveate sculpture; malar sulcus distinct, complete; gena convex, genal carina usually absent, at most present as slight angulation near oral fossa. Antennal scape at least  $1.2\times$  longer than first funicular segment, anellus transverse to quadrate, 6 funicular segments longer than wide, becoming quadrate apically, F6 usually appressed to clava but distinct (Fig. 60); clava with 3 fused segments; first funicular segment tapered at base, usually  $\sim 1.5\times$  longer than broad; funicular segments and clava with 1–2 irregular, overlapping rows of longitudinal sensilla (MPS), covered with subdecumbent setae, about  $0.8\text{--}1.0\times$  width of corresponding segment; apex of clava with fine ‘crown’ of microsetae, sometimes directed apicoventrally (Fig. 60; see *I. azofiefai*, *I. colombia*). Head posteriorly with lateral foraminal plates distinct dorsally, indistinct laterally, extending no more than  $1/4$  length postgenal bridge sulci; postgenal bridge sulci deep and complete, bridge ornamented with digitiform cuticular expansions; postgenal present, straight, indistinct dorsally, postgenal lamina absent (cf. Figs. 34–36). **Mesosoma:** About twice as long as wide (length  $2.3\text{--}2.7\times$  width), dorsal surface quite straight in lateral view, scutellum flat (Fig. 75), propodeum usually sloping gently downward, anterior  $1/2$  nearly coplanar with scutellum; notauli typically obliterated posteriorly and indicated ante-

riorly by shallow groove or sculpture; axillular groove obliterated anteriorly, deep posteriorly; lateral surface of prepectus triangular, narrow posteriorly, with posterior corner rounded; subventral carina of prepectus visible in lateral view; epicnemium in lateral view broad and evenly curved, without a differentiated mesopleural shelf (just a simple transverse carina in front of mesocoxae; Fig. 77); femoral depression of mesopleuron shallowly concave, usually demarcated anteriorly by adscrobal carina (rarely absent). Procoxa convex anteriorly, laminate anteroapically (Fig. 75); metafemur about  $3\times$  as long as wide; metatibia with two pointed, apical spurs. Fore wing with postmarginal vein longer than marginal vein, stigmal vein slightly shorter than marginal vein, speculum and basal cell setose (like rest of wing) (Figs. 76, 79). Metasoma: with petiole usually asetose, but some sometimes (*I. brasiliensis*, *I. parkeri*) with paired fine setae anterodorsally, and usually subequal to longer than broad (elongate in *I. similis*); gaster elongate (length  $2.7\text{--}4.0\times$  height), sclerotized, usually not collapsing and often compressed dorsoventrally (especially anteriorly) such that cross section is triangular to ovate; gastral terga 3–6 usually somewhat similar in length with 1–2 shortest; hypopygium nearly always at midlength of gaster, ventral line with 2–4 pairs of setae; ovipositor sheaths slightly tilted upward at apex, terminating posterad Gt7.

**Males.**—Presently known for seven of eight species (unknown for *I. paradoxus*). Usually slightly smaller and darker (especially gaster) than female. Antennal scape lacking any light-colored oval area at apex (opposite insertion of pedicel), flagellomeres either parallel sided or asymmetrically pedicellate, usually at least somewhat narrowed at each end, with erect setae at least  $1\text{--}4\times$  width of corresponding flagellomere (Figs. 61, 62, 66).

**Comments.**—The number of setae on the apex of the hypopygium is a fairly reliable

and previously unreported means of separating *Bephrata* (5 or more pairs of setae) from *Isosomodes* (2–4 pairs); the only exception is *B. citri*, which appears to have only three pairs of setae, although this is based on the observation of just one specimen (the only specimen with an exposed hypopygium).

**Biology.**—The specimens examined were collected by Malaise trap, hand net, canopy fogging and, less commonly, rearing from eggs; none were collected at lights. The only host record is of *I. gigantea*, from eggs of *Bucrates capitatus* (De Geer) (Orthoptera: Tettigoniidae).

**Distribution.**—In the New World, species of *Isosomodes* have been collected from USA (Maryland) to Ecuador. They occur primarily in the lowlands with some species occurring at mid altitudes.

*Isosomodes azofiefai* Gates and Hanson, **n. sp.**  
(Figs 20, 60, 61, 75–78)

**Female holotype.**—Body length 6.0 mm. Color: Black: F5–F6, clava, head, collum, most of gaster; dark orange: mesosoma except median channel of propodeum blackish; golden: F1–F3 (scape, pedicel, and F4 dusky), tegula, legs, Gt1–2 laterally and ventrally, Gt1 with dorsal spot (Fig. 20). Head:  $1.4\times$  as broad as high, clypeus with apical margin straight, slightly notched; malar space and gena finely reticulate with foveae more widely spaced, clypeus smooth; anterior tentorial pits present, small; malar space  $0.5\times$  eye height; scrobal basin carinate ventrolaterally; ratio of lateral ocellus:ocellular distance:postocellar distance as  $10:5:22$ ; antenna (Fig. 60) with scape barely reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus: F1:F2: F3:F4:F5:F6:club as  $42:14:5:20:15:16:15:13:12:33$ ; funiculars longer than broad; F1 slightly narrowed basally, plate sensilla present in basal  $1/3$ ; clava bisegmented, fused, with apical pilosity directed anteroventrally (Fig. 60). Mesosoma:  $2.5\times$  as long



as broad, pronotum  $1.1\times$  as long as broad, mid lobe of mesoscutum  $1.4\times$  as long as broad, scutellum  $1.1\times$  as long as broad; notauli impressed anteriorly, obliterated posteriorly, axillar grooves deep posteriorly, internalized anteriorly and not visible; femoral depression smooth subfoveolate; metapleuron deeply foveate; propodeum foveate, with narrow, laterally carinate median channel, incomplete cross carinae along its length; mesopleuron somewhat smooth anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; ratio metatibia: metatarsomeres as 115:45:20:16:6:12; ratio marginal vein:postmarginal vein:stigmatal vein as 30:75:25 (Fig. 76). **Metasoma:** "humpbacked" in lateral view, ovipositor directed slightly dorsad horizontal (Fig. 77); gaster about  $3.5\times$  as long as high, gastral petiole  $0.6\times$  as long as broad, dorsally rugose and produced anterolaterally into flattened prongs; ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 20:17:32:46:23:50:18:10; hypopygium reaching  $0.6\times$  length of gaster, apical region of ventral line with 2 pairs of setae.

**Male.**—Body length 4.7 to 6.0 mm. **Color:** as for female, except yellow areas of gaster described for female more extensive ventrally (Fig. 78); scape and pedicel dusky, flagellum entirely black; flagellar segments (Fig. 61) pedicellate with a basal and an apical whorl of erect setae each  $3-4\times$  as long as width of segment; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:club as 38:10:3:38:33:35:34:30:25:30. Gastral petiole  $2.4\times$  as long as broad, broadest medially, reticulate dorsally fading to glabrous ventrally, subequal in length to metacoxa; ratio of petiole (dorsal length measured in lateral view), Gt1–Gt7 (all measured dorsally): 61:22:15:27:50:32:30:11.

**Diagnosis.**—This species is unique in that the female clava is angulate apically. The males are similar to *I. landoni*, except the flagellomeres are asymmetrically sided with setae  $2-3\times$  the length of the corre-

sponding segment (parallel-sided and  $\leq 2\times$  in *I. landoni*).

**Variation.**—Female length ranges 5.5–7.5 mm and in extent of maculation that is present in the median channel of and posterodorsally on the propodeum, and laterally on the gaster. Occasionally, F4 is dusky. Male coloration varies primarily in the extent of the darker maculation on the propodeal/scutellar region and on the dorsum of the gaster.

**Type specimens.**—Holotype, ♀ (USNM). COSTA RICA, Puntarenas, Golfo Dulce, 24 km W. Piedras Blancas, 200 m, iii–v.1989, P. Hanson.

Paratypes, 18♀ 16♂: COSTA RICA, Alajuela, San Carlos, La Fortuna, PN Arenal, Sector Catarata, 500 m, 15.iii–24.iv.2001, G. Carballo, L\_N\_4625000\_268500, #62077 (1♂, INBio); Guanacaste, Bagaces, Parque Nacional Palo Verde, Sector Catalina, Fila Catalina, 200 m, 09.iv–v.2001, Jiménez, Malaise, L\_N\_2574000\_400000, #62262, INBio CRI0003704900 (1♀, INBio); Parque Nacional Guanacaste, 9 km S. Sta. Cecilia, Estación Pitilla, 700 m, 31.iii–15.iv.1992, P. Rios, L\_N\_330200, 380200, INBio CRI000771498 (1♂, INBio); Heredia, Puerto Viejo, La Selva, 100 m, I.1991, J. Noyes (1♀, BMNH); 3 km S. Puerto Viejo, OTS-La Selva, 100 m, 17.vii.1995, P. Hanson (1♀, MZCR); same as preceding, but viii–ix.1993 (1♀, MZCR); Limón, Sector Cerro Cocori, Fca. de E. Rojas, 150 m, xii.1992, L\_N\_286000\_567500, INBio CRI000961112 (1♀, INBio); next four same as preceding, but 12.iv–19.v.1992, INBio CRI000469958 (1♀, INBio); 9–30.xi.1992, INBio CRI000862271 (1♂, INBio); 12–31.viii.1992, INBio CRI000760508 (1♂, INBio); viii.1992, INBio CRI000581661 (1♂, INBio); x.1991, INBio CRI000462179 (1♂, INBio); Valle de la Estrella, Reserva Biológica Hitoy Cerere, Sendero Toma de Agua, 140 m, 8.v.1999, F. Umaña, L\_N\_184300\_643500, #54234, INBio CRI0003704896 (1♂, INBio); Valle de la Estrella, Reserva Biológica Hitoy Cerere, Sendero Toma de Agua, 100 m, 19.x–19.xi.2000, F. Umaña, L\_N\_184300\_643500, #60668, INBio CRI0003705086 (1♂, INBio); Reserva Biológica Hitoy Cerere, Estación Hitoy Cerere, Send. Bobocara, 300 m, 19.x–19.xi.2000, F. Umaña, Malaise L\_S\_184550\_641800, # 60669 (1♀, MZCR); Puntarenas, Gofito, Jiménez, Parque Nacional Corcovado, Río Corcovado, 50 m, 22.iii.2001, J.

Azofiefa, Malaise, L\_S\_503500\_282500, # 61709 (1♂, USNM); Golfito, Estación Agujas, Cerro Rincón, 645–745 m, 15.iv–v.2000, J. Azofiefa, L\_S\_275500\_521950, #56675, INBio CRI0003705092 (1♂, INBio); Golfito, Parque Nacional Corcovado, Estación Agujas, Charcos, 600 m, 17.iv–16.v.1999, J. Azofiefa, L\_S\_276350\_523500, #52776, INBio CRI0003704891 (1♂, INBio); Parque Nacional Corcovado, Estación Sirena (ACOSA), 1–100 m, 5–23.iv.1995, A. Picado, L\_N\_270500\_507900, #4552, INBio CRI000218418 (1♀, INBio); Parque Nacional Corcovado, Estación Sirena, 0–100 m, xi.1993, G. Fonseca, L\_S\_270500\_508300, #2490, INBio CRI000625202 (1♀, INBio); Parque Nacional Corcovado, Queb. La Bonanza, 500 m, 15.iii–28.iv.2001, L\_S\_524800\_275700, #62430, INBio CRI0003704902 and INBio CRI0003704906 (2♂, INBio); RF Golfo Dulce, 24 km W. Piedras Blancas, 200 m, vi–vii.1991, P. Hanson (1♀, USNM), ix.1992 (1♀, MZCR), iii–vi.1990 (1♀, 2♂, USNM), vi–viii.1989 (1♀, USNM), xi.1990 (1♀, MZCR), iii.1992 (1♀, MZCR); Golfo Dulce, 24 km W. Piedras Blancas, 200 m, vi–viii.1989, P. Hanson (1♂, BMNH); Golfo Dulce, 10 km W. Piedras Blancas, 100 m, iii–v.1989, P. Hanson (1♀, BMNH); Península de Osa, Rancho Quemado, 200 m, 12–24.v.1993, A. Gutiérrez, L\_S\_292500\_511000, INBio CRI001189470 (1♂, INBio); P. N. Manuel Antonio, Quepos, 80 m, v–vi.1991, G. Varela and R. Zuniga, L\_S\_370900\_448800 #7441 (2♀, 1♂, INBio).

*Etymology*.—This species is named for Antonio Azofiefa, an excellent INBio parataxonomist, whose assistance in the field and perceptive collecting has been a great help to us in conducting our research.

*Host*.—Unknown.

*Distribution*.—Costa Rica.

*Isosomodes colombia* Gates and Hanson, *n. sp.*  
(Figs 22, 66, 79)

*Female holotype*.—Body length 5.1 mm. *Color*: golden—face, scape, gena dorsally, postgena, pronotum, fore legs, mesoscutum, middle legs, mesopleuron dorsally, scutellum in anterior 2/3, metatarsus, tip of ovipositor sheaths; pale yellow—metafemur, Gt3 except thinly brown anteriorly and posteriorly; black—vertex, occiput dorsally, scutellum laterally and in posterior 1/3, propodeum, petiole, Gt1;

brown—lower face faintly suffused, malar space, pedicel, flagellum, pro- and metafemora suffused basally, collum, mesopleuron in ventral 2/3, metacoxae, metafemora with faint spot apicolaterally, metatibiae, Gt2, Gt4–Gt7 (Fig. 22). *Head*: 1.3× as broad as high, clypeus with radiating carinae sparse, fine, margin straight; anterior tentorial pits small; intertorular space elongate sharply triangular, with 1–2 setae along midline, dorsally continuous as intrascrobal lamina in basal fourth scrobal depression, carina absent in dorsal three-fourths; malar space 0.4× eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellocular distance:postocellar distance as 10:5:22. Antenna with scape barely reaching ventral margin of anterior ocellus; ratio of scape (minus radicle): pedicel:anellus:F1:F2:F3:F4:F5:F6:club as 33:10:2:17:14:14:13:13:11:22; funicles longer than broad; F1 slightly narrowed basally, MPS present in basal 1/3; clava bisegmented, fused, apically slightly truncate and pilose. *Mesosoma*: 2.3× as long as broad, pronotum 0.9× as long as broad, mid lobe of mesoscutum 1.3× as long as broad, scutellum about as long as broad; axillar grooves deep posteriorly, apparently internalized anteriorly and not visible; mesopleuron foveolate anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; metapleuron umbilicately punctate; propodeum with distinct median groove composed of line of asetose foveae delimited laterally carinae; ratio metatibia: metatarsomeres as 98:35:15:10:8:10; ratio marginal vein:postmarginal vein:stigmatal vein as 20:80:41 (Fig. 79). *Metasoma*: bluntly tapered in lateral view, ovipositor directed horizontally; gastral petiole 0.8× as long as broad, dorsally rugose and produced anterodorsally into a transverse carina; gaster about 3.0× as long as high, ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 23:10:55:60:45:55:30:14.

*Male*.—Body length 4.3 mm. *Color*: as for female, except scape with slightly swollen area apically, flagellum becoming pale



brown apically, beginning with F5. Sculpture as for female. Flagellomeres pedicellate with a whorl of erect setae apically and basally, each about  $3.0\text{--}4.0\times$  as long as width of flagellomere; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:club as  $33:8:1:21:28:28:25:20:23$  (Fig. 66). Gastral petiole  $2.1\times$  as long as broad, broadest medially, finely rugulose dorsally, subequal in length to metacoxa; ratio Gt1–Gt7 (all measured dorsally):  $20:25:40:33:35:28:10$ .

**Variation.**—The female paratype has the scutellum black and the band on Gt2 narrower dorsally and is missing the left flagellum. The male paratype is missing the left flagellum beyond F1 and one fore leg is mounted separately on the same point.

**Type specimens.**—Holotype ♀ (IAVH): COLOMBIA, Amazonas, Parque Nacional Natural Amacayacu Matamata, San Martín, 150 m,  $3^{\circ}23'01''\text{N}$   $70^{\circ}06'01''\text{W}$ , 10–18.X.2000, B. Armado, M.835.

Paratypes, 1♀, 1♂ (USNM): same data as for holotype except dates: 2–10.X.2000 (1♀); 1–8.IX.2000 (1♂).

**Etymology.**—This species is named for its country of origin, Colombia.

**Host.**—Unknown.

**Distribution.**—Colombia.

*Isosomodes gigantea* (Ashmead)  
(Figs 21, 59, 67–70)

*Isosoma gigantea* Ashmead 1886: 127. Holotype ♂, by monotypy [Jacksonville, FL].

*Isosomodes gigantea*: Ashmead 1894: 332 [In: Riley et al. 1894].

*Isosomodes brasiliensis* Ashmead 1904: 460–461. Lectotype ♀, designated below, (USNM). N. syn.

**Male holotype.**—Body length 4.1 mm. **Color:** brown except following areas golden—scape, anterolateral pronotum, fore and middle leg, hind leg distad coxa, tegulae (Fig. 73). **Head:**  $1.3\times$  as broad as high, few fine carinae radiating from clypeus; clypeus shallowly notched; supra-clypeal area with fine elongate reticulation;

anterior tentorial pits present, small; malar space  $0.7\times$  eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellular distance:postocellar distance as  $8:11:24$ . Antenna with scape reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:F6:club as  $30:8:2:33:25:22:24:22:22:30$ ; funicles elongate, parallel sided, F1 MPS absent in basal  $1/2$ ; F2–6 with two sparse, irregular rows of plate sensilla; clavomeres fused. **Mesosoma:**  $2.3\times$  as long as broad, pronotum  $0.8\times$  as long as broad, mid lobe of mesoscutum  $1.8\times$  as long as broad, scutellum approximately as long as broad; notauli impressed anteriorly, obliterated posteriorly, axillar grooves deep posteriorly, internalized anteriorly and not visible; femoral depression subfoveolate; metapleuron deeply foveate; propodeum foveate with indistinct median groove composed of line of asetose foveae delimited laterally by setose foveae; ratio metatibia: metatarsomeres as  $95:45:15:10:8:15$ ; ratio marginal vein:postmarginal vein:stigmatal vein as  $32:60:45$ . **Metasoma:** evenly tapered in lateral view; gaster  $2.3\times$  as long as high, gastral petiole  $2.0\times$  as long as broad, carinate-rugose dorsally (Fig. 67); ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally):  $20:17:32:46:23:50:18:10$ .

**Female.**—Body length 4.2 to 6.0 mm. **Color:** as for male, except pedicel–F5 golden, only F6+clava brown. Flagellar segments (Fig. 68) elongate to quadrate and of uniform width, evenly covered with decumbent setae each  $\sim 1.0\times$  as long as width of corresponding segment; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:F6:club as  $34:10:3:18:15:15:14:13:11:20$ . Gastral petiole  $0.75\times$  as long as broad, broadest medially, rugulose dorsally and ventrally (Fig. 67),  $0.5\times$  length of metacoxa; ratio of petiole (dorsal length measured in lateral view), Gt1–Gt7 and ovipositor sheaths (all measured dorsally):  $16:25:30:42:40:70:23:8$ .

**Diagnosis.**—This species is most similar to *I. similis*, but is separated by having a

shorter petiole in the female and male flagellomeres brown versus a petiole  $>1.0\times$  as long as broad.

*Variation*.—Female length ranges 4.0–6.5 mm. The body coloration across all specimens is uniformly dark brown to black with occasional infuscation on the legs and flagellomeres.

*Type specimen of I. gigantea*.—Holotype ♂, by monotypy (USNM): UNITED STATES, Florida, Jacksonville, Type No. 2839 U.S.N.M.

*Type specimens of I. brasiliensis*.—Lectotype ♀, here designated (USNM): May, Corumba, Type No. 8077 U.S.N.M. (Brazil) (missing right antenna beyond F3, left antenna beyond F2).

Paralectotypes, 2♀ (USNM), same data as for lectotype. Note: Five specimens were indicated in Ashmead's original description, but the other two former syntypes have not been located.

*Other specimens examined*.—COSTA RICA, Alajuela, Chiles de Aguas, Zarcas Café, 300 m, xii.1989, R. Céspedes (1♀ MZCR); Finca La Selva, NE Dos Rios, 400 m, 27.iii.1988, Hanson (2♂ MZCR); Inst. Tec. Santa Clara, 150 m, 24.iii.1989, Hanson & Godoy (1♂ MZCR); Guanacaste, Cerro el Hacha, NW Volcán Orosi, 300 m, 1988 (7♀ MZCR); Estación Mengo, SW Volcán Cacao, 1100 m, 1988–1989 (1♀, 1♂ MZCR); same data but ix–x.1989 (1♀ MZCR); v.1988 (1♀ MZCR); Santa Rosa National Park, Hacienda 1-0 (1♀ MZCR); same data but i.1987, Gauld (2♀ BMNH); Santa Rosa National Park, Hacienda 4-C, xii.1986–1.1987 (1♀ MZCR); Heredia, 3 km S. Puerto Viejo, OTS-La Selva, 100 m, x.1992, P. Hanson (1♀ MZCR); Puntarenas, Península de Osa, 5 km N. Puerto Jiménez, 10 m, iii–iv.1991, Hanson & Godoy (1♀ BMNH); same data but collector Hanson and dates: i.1992 (1♀ BMNH); iii.1992 (1♀ BMNH); iv.1992 (1♀ BMNH); iv.1993 (1♀ BMNH); v.1993 (1♀ BMNH); RF Golfo Dulce, 24 km W. Piedras Blancas, 200 m, iii.1992, P. Hanson (1♀ MZCR). COLOMBIA, Armenia Quindio, 8.viii.1974, R. Cárdenas, ex cricket egg (1♀, USNM). DOMINICA, Castle Comfort, 12.ix.1965, D.L. Jackson, Bredin-Archbold-Smithsonian Biological Survey (1♂, USNM). HONDURAS, La Ceiba, 6.viii.1916, F.J. Dyer, Sweep weeds, No. 8743 to 8872 (3♀, 4♂, USNM). PANAMA, Fort Clayton, xii.1946, N.L.H. Krauss (1♀, USNM). SAINT VINCENT AND THE GRENADINES, St. Vincent, H.H. Smith (1♀, USNM). TRINIDAD

AND TOBAGO, Goldborough, 19–26.v.1994, M. J. Sommeijer, malaise trap in neglected citrus orchard bordering on primary forest (6♀, USNM), same data with different dates: 17.ii–26.v.1994 (11♀, 2♂, USNM); 24.ii–3.iii.1994 (8♀, 4♂, USNM); 24–31.iii.1994 (1♀, USNM); 31.iii–17.iv.1994 (3♀, 1♂, USNM); 14–21.iv.1994 (1♀, 2♂, USNM); 21–28.iv.1994 (6♀, USNM); 28.iv–5.v.1994 (3♀, USNM); 5–12.v.1994 (1♂, USNM). UNITED STATES, Florida, Jacksonville (2♂, USNM); District of Columbia (1♀, 1♂, USNM); Maryland, Mayo Beach, 30.vii.1944, H.K. Townes (1♂, USNM). VENEZUELA, Zulua, El Tucuco, 45 km SW Machiques, 5–6.vi.1976, A. Menke and D. Vincent (1♂, USNM); 6 km W La Concepcion, 18.vi.1976, A. Menke and D. Vincent (1♂, USNM); Los Angeles del Tucuco, 16.iv.1981, E. Grissell, sweep rain forest (1♀, 1♂, USNM); Tucupido, El Maracay [handwriting difficult to read], 22.v.1957, C.J. Rosales, ex egg of *Bucrates capitatus* (3♀, 2♂, USNM).

*Host*.—Reared eggs of *Bucrates capitatus* (Orthoptera: Tettigoniidae).

*Distribution*.—Colombia, Dominica, Honduras, Panama, Saint Vincent and The Grenadines, Trinidad and Tobago, United States (Florida, Maryland), and Venezuela.

*Isosomodes landoni* Gates and Hanson, n. sp.  
(Figs 23, 62)

*Female holotype*.—Body length 4.5 mm. Color: golden except the following brown—clava and propodeum anterolaterally (Fig. 23). Head:  $1.3\times$  as broad as high, clypeus with radiating carinae absent, smooth; anterior tentorial pits small; malar space  $0.6\times$  eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellular distance:postocellar distance as 9:11:23; antenna with scape barely reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus: F1:F2: F3:F4:F5:F6:club as 35:12:2:22:15: 15:14:12:10:16; funicles longer than broad; F1 slightly narrowed basally, MPS absent in basal  $1/3$ ; clava bisegmented, fused, apically radially pilose. Mesosoma:  $2.4\times$  as long as broad, pronotum about as long as broad, mid lobe of mesoscutum  $1.3\times$  as



long as broad, scutellum about as long as broad; axillar grooves deep posteriorly, apparently internalized anteriorly and not visible; mesopleuron foveolate anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; metapleuron umbilicately punctate; propodeum with distinct median groove composed of line of asetose foveae delimited laterally carinae; ratio metatibia: metatarsomeres as 105:38:15:10:5:15; ratio marginal vein:postmarginal vein:stigmatal vein as 30:62:28. Metasoma: bluntly tapered in lateral view, ovipositor directed horizontally; gastral petiole  $1.1\times$  as long as broad, dorsally rugose and produced anterodorsally into flattened, faintly pointed carina; gaster about  $3.9\times$  as long as high, ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:28:28:45:32:40:16:3.

*Male*.—Body length 4.4–4.7 mm. Color: as for female, except flagellum brown. Sculpture as for female. Flagellomeres (Fig. 62) filiform with 5–6 whorls of erect setae each about  $2.0\times$  as long as width of flagellomere; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:F6:club as 35:10:2:32:30:25:24:24:24:30. Gastral petiole  $2.0\times$  as long as broad, broadest medially, rugulose-reticulate dorsally with irregular carina posteroventrally, subequal in length to metacoxa; ratio Gt1–Gt7 (all measured dorsally): 20:30:41:44:28:20:10.

*Variation*.—Female length ranges 3.4–5.5 mm.

*Type specimens*.—Holotype, ♀ (USNM): UNITED STATES, Maryland, Calvert County, American Chestnut Land Trust, Warrior's Rest Sanctuary, 38.5360641–76.5175095, 28.vii–12.viii.2006, M. Gates, Malaise trap residue.

Paratypes, 6♀, 2♂ (USNM): same data as for holotype (6♀, 1♂); North Carolina, Onslow Co., Ashe Island, 19 Aug. 1975, J. C. Dukes, on *Spartina cynosuroides* (1♂).

*Etymology*.—This species is named for Landon Gates, the youngest son of MG.

*Host*.—Unknown. Possible hosts include several species of *Conocephalus* and *Orchelimum* (Orthoptera: Tettigoniidae) associat-

ed with habitats along the Atlantic seaboard where they oviposit in stems of various grasses and sedges.

*Distribution*.—United States (Maryland and North Carolina).

*Isosomodes nigriceps* Ashmead  
(Figs 24, 63)

*Isosomodes nigriceps* Ashmead 1904: 461. Holotype ♂, by monotypy. Santarem, Brazil (USNM).

*Male holotype*.—Body length 2.5 mm. Color: golden except the following brown—vertex and scrobal depression dorsally (Fig. 24). Head:  $1.3\times$  as broad as high, clypeus with radiating carinae absent, smooth; anterior tentorial pits small; malar space  $0.6\times$  eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellocular distance:postocellar distance as 9:11:23; antenna with scape barely reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:[F5:F6:club; missing in lectotype] as 35:12:2:22:15:15:14; funicles longer than broad, pedicellate with a basal and an apical whorl of erect setae each  $2\text{--}3\times$  as long as width of segment. Mesosoma:  $2.4\times$  as long as broad, pronotum about as long as broad, mid lobe of mesoscutum  $1.3\times$  as long as broad, scutellum about as long as broad; axillar grooves deep posteriorly, apparently internalized anteriorly and not visible; mesopleuron foveolate anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; metapleuron umbilicately punctate; propodeum with distinct median groove composed of line of asetose foveae delimited laterally carinae; ratio metatibia: metatarsomeres as 105:38:15:10:5:15; ratio marginal vein:postmarginal vein:stigmatal vein as 30:62:28. Metasoma: [missing in holotype].

*Female*.—Unknown.

*Type specimen*.—Holotype ♂ (USNM): BRAZIL, Santarem, H. H. Smith coll., Type No. 60508 USNM. This specimen is also missing its right antenna beyond the anellus, right fore

leg, left fore leg, tarsomeres 3–5, left middle and hind legs and right hind leg beyond coxa. Originally indicated as described from a single specimen (Ashmead 1904).

*Host*.—Unknown.

*Distribution*.—Brazil.

*Isosomodes paradoxus* Gates and Hanson, **n. sp.**  
(Figs 25, 57–58)

*Female holotype*.—Body length 5.7 mm. Color: golden except the following black—ocellar triangle, median line on pronotum and mesoscutum, propodeum medially, metasternum, midline Gt1–Gt4, Gt4 in apical 1/2 through Gt7 (Fig. 25). Head: 1.3× as broad as high primarily reticulate with few irregular, shallow umbilicae, malar space and gena finely reticulate with umbilicae more widely spaced, clypeus acarinate, smooth, shallowly bilobate; anterior tentorial pits small; intertorular space elongate triangular, with a few setae along midline, dorsally continuous as intrascrobal lamina in basal fifth scrobal depression, carina fading dorsally; malar space 0.4× eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellular distance:postocellar distance as 10:8:25, ocellar triangle depressed. Antenna with scape exceeding ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus: F1:F2:F3:F4:F5:F6:club as 35:18:5:21:19:19:16:14:22; funicles longer than broad; F1 slightly narrowed basally, MPS absent in basal fifth; clava bisegmented, fused, apically radially pilose. Mesosoma: 2.4× as long as broad, pronotum 0.7× long as broad, mid lobe of mesoscutum 1.8× as long as broad, scutellum about as long as broad; axillar grooves deep posteriorly, apparently internalized anteriorly and not visible; mesopleuron foveolate anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; metapleuron umbilicately punctate; propodeum with distinct median groove composed of line of asetose foveae delimited laterally carinae; ratio metatibia: metatarsomeres as 104:44:15:10:8:15; ratio

marginal vein:postmarginal vein:stigmatal vein as 25:60:36. Metasoma: bluntly tapered in lateral view, ovipositor directed horizontally; gastral petiole 1.2× as long as broad, dorsally rugose, submedially bicarinate; gaster about 4.0× as long as high, ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:30:43:50:37:70:23:8.

*Male*.—Unknown.

*Type specimen*.—Holotype, ♀ (USNM): ECUADOR, Napo, Tiputini Biodiversity Station, 216 m, 00°37'55"S, 76°08'39"W, 6.ii.1999, T. Erwin et al., fogging of mostly bare green leaves, some with covering of lichenous or bryophytic plants, Lot # 2068.

*Etymology*.—This species is named for its paradoxical nature in sharing certain diagnostic features of both *Isosomodes* and *Bephrata*.

*Host*.—Unknown.

*Distribution*.—Ecuador.

*Isosomodes parkeri* Gates and Hanson, **n. sp.**  
(Figs 26, 64–65)

*Female holotype*.—Body length 5.7 mm. Color: golden except the following black—flagellum, vertex excluding spot posterolaterad lateral ocellus, pronotum dorsally, mesoscutum excluding lateral 1/2 lateral lobe, mesopleuron ventrally, metapleuron, scutellum, metacoxa laterally and mesally, propodeum, petiole, Gt1–Gt6 dorsally, syntergum in dorsal 2/3, ovipositor sheaths apically (Fig. 26). Head: 1.4× as broad as high, clypeus with fine radiating carinae; anterior tentorial pits small; malar space 0.6× eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellular distance:postocellar distance as 9:12:22. Antenna with scape barely reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus: F1:F2: F3:F4:F5:F6:club as 30:12:2:21:15:15: 14:14:12:19; funicles longer than broad; F1 slightly narrowed basally, MPS absent in basal 1/3; clava bisegmented, fused, apically radially pilose. Mesosoma: 2.4× as long as broad, pronotum about as long as



broad, mid lobe of mesoscutum  $1.3\times$  as long as broad, scutellum about as long as broad; axillar grooves deep posteriorly, apparently internalized anteriorly and not visible; mesopleuron foveolate anteriorly, bordered by irregular foveae, becoming glabrous posteroventrally and striate posterodorsally; metapleuron umbilicately punctate; propodeum with distinct median groove composed of line of asetose foveae delimited laterally carinae; ratio metatibia: metatarsomeres as 104:44:15:10:8:15; ratio marginal vein:postmarginal vein:stigmatal vein as 25:60:36. Metasoma: bluntly tapered in lateral view, ovipositor directed horizontally; gastral petiole  $1.2\times$  as long as broad, dorsally rugose, submedially bicarinate; gaster about  $4.0\times$  as long as high, ratio of Gt1–Gt7, ovipositor sheath (all measured dorsally): 25:30:43:50:37:70:23:8.

Male.—Body length 4.4 mm. Color: as for female (Fig. 64), except flagellum brown. Sculpture as for female. Flagellomeres (Fig. 65) filiform with numerous erect setae each about  $1.0\times$  as long as width of flagellomere; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:F6:club as 30:10:2:37:28:28:25:24:2:30 (Fig. 65). Gastral petiole  $2.4\times$  as long as broad, broadest medially, rugulose dorsally and ventrally, subequal in length to metacoxa; ratio Gt1–Gt7 (all measured dorsally): 20:26:22:32:16:20:11.

Variation.—Female length ranges 5.5–5.7 mm, but vary little in coloration.

Type specimens.—Holotype, ♀ (USNM): UNITED STATES, Maryland, Calvert County, American Chestnut Land Trust, Warrior's Rest Sanctuary, 38.5360641–76.5175095, 28.vii–12.viii.2006, M. Gates, Malaise trap residue.

Paratypes, 3♀, 1♂ (USNM): same data as for holotype.

Etymology.—This species is named after William Parker, one of the original founders (in 1649) of Anne Arundel County, Maryland. The watershed with which this species is associated, Parker's Creek, is named after him.

Host.—Unknown. Possible hosts include several species of *Conocephalus* and *Orche-*

*limum* (Orthoptera: Tettigoniidae), that are associated with habitats along the Atlantic seaboard where they oviposit in stems of various grasses and sedges.

Distribution.—United States (Maryland).

*Isosomodes similis* Gates and Hanson, n. sp.  
(Figs 71–74)

Female holotype.—Body length 5.2 mm. Color: brown except following areas golden—scape, pedicel, F1–F5, anterolateral pronotum, tegula, fore leg, middle leg, metasomal leg except basal  $\frac{3}{4}$  metacoxa (Fig. 72). Head:  $1.3\times$  as broad as high, few fine carinae radiating from clypeus; clypeus shallowly notched; supraclypeal area with fine elongate reticulation and setigerous foveae; anterior tentorial pits present, small; malar space  $0.6\times$  eye height; scrobal basin carinate laterally; ratio of lateral ocellus:ocellular distance:postocellar distance as 10:10:18. Antenna with scape reaching ventral margin of anterior ocellus; ratio of scape (minus radicle):pedicel:anellus: F1:F2: F3:F4:F5:F6:club as 33:15:2:20:15: 15:14:12:30; funicles elongate; F1 slightly narrowed basally, MPS absent in basal  $1/3$ ; F2–5 with two or more staggered rows of plate sensilla. Mesosoma:  $2.7\times$  as long as broad, pronotum  $0.9\times$  as long as broad, mid lobe of mesoscutum  $1.8\times$  as long as broad, scutellum approximately as long as broad; notauli impressed anteriorly, obliterated posteriorly, axillar grooves deep posteriorly, internalized anteriorly and not visible; femoral depression rugulose subfoveolate; metapleuron deeply foveate; propodeum foveate with indistinct median groove composed of line of asetose foveae delimited laterally by setose foveae; ratio metatibia: metatarsomeres as 90:38:15:10: 8:10; ratio marginal vein:postmarginal vein:stigmatal vein as 33:73:35. Metasoma: evenly tapered in lateral view, ovipositor parallel to horizontal; gaster  $2.7\times$  as long as high, gastral petiole  $1.5\times$  as long as broad, asetose dorsolaterally, dorsally rugulose (Fig. 71); ratio of Gt1–Gt7, oviposi-

tor sheath (all measured dorsally): 15:20:43:45:35:70:20:10; hypopygium reaching  $0.5\times$  length of gaster, apical region of ventral line with 3 pairs of setae.

**Male.**—Body length 4.2 to 5.5 mm. **Color:** as for female except F6 brown and metafemur brown. Flagellar segments (Fig. 73) elongate and of uniform width, evenly covered with suberect setae each  $\sim 1.0\times$  as long as width of corresponding segment; ratio scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:F6:club as 30:10:2:32:26:24:22:20:20:26. Gastral petiole  $2.0\times$  as long as broad, broadest medially, rugulose dorsally and ventrally (Fig. 74), with row of two anteriorly-directed setae present dorsolaterally,  $0.8\times$  length of metacoxa; ratio of petiole (dorsal length measured in lateral view), Gt1–Gt7 (all measured dorsally): 45:40:20:20:25:20:20:11.

**Diagnosis.**—This species is most similar to *I. gigantea*, but is separated by the length of the female petiole. The males are similar to *I. landoni*, except the flagellomeres are asymmetrically sided with setae  $2\text{--}3\times$  the length of the corresponding segment (parallel-sided and  $\leq 2\times$  in).

**Variation.**—Female length ranges 3.8–6.5 mm. The body coloration across all specimens is uniformly dark brown to black with occasional infuscation on the legs (particularly the metafemur) and flagellomeres. Although not seen in the holotype, most females possess two fine setae anterodorsally on the petiole

**Type specimens.**—Holotype, ♀ (USNM): COSTA RICA, Heredia, 3 km S. Puerto Viejo, OTS-La Selva, 100 m, x.1992, P. Hanson.

Paratypes, 25♀, 19♂: 7♀, 8♂: same data as holotype (1♀ USNM); different dates: ix.1992 (2♀, 1♂ USNM); iii–iv.1993 (3♀, 3♂ USNM); iv–v.1993 (1♀, 1♂ USNM); vi.1993 (1♂ USNM); different dates and collectors (Hanson & Godoy): ii–iv.1993 (3♂ USNM); F. La Selva, 3 km S Puerto Viejo, 10°26'N 84°01'W, 26.iii.1984, H. A. Hespeneheide, at foliar nectaries *Byttneria aculeata* (1♀ USNM); Estación Biológica La Selva, 50–150 m, 10°26'N 84°01'W, Proyecto ALAS, INBio-OET, M/01/320,

15.i.1994, parcelas sucesionales (1♀, INBio); Estación Biológica La Selva, 50–150 m, 10°26'N 84°01'W, INBio -OET, i.2000, CRI002623432 (1♀, INBio); same data but, xii.1999, CRI002623420 (1♀, 1♂ INBio); Chilamate, 75 m, 4.ii.1989, Hanson & Godoy (1♂ USNM); Alajuela, Res. Biológica Alberto Brenes (San Ramon), 900 m, viii–ix.1995 (5♀, 2♂ MZCR); same data but vii–viii.1995 (1♀ MZCR); Estación Biológica San Ramón, viii–ix.1995 (3♀, 3♂ MZCR); same data but vii–viii.1995 (1♀, 1♂ MZCR); Cartago, Rio Chitaria, NE de Jabillos, 750 m, 28.iv.1988, P. Hanson (1♂ USNM); Guanacaste, Estación Pitilla, 9 km S. Santa Cecilia, 700 m, vi.1988, P. Hanson (1♀ MZCR); same data but v.1988 (1♀ MZCR); Limón, 16 km W. Guapiles, 400 m, vii–ix.1990, P. Hanson (1♀ MZCR); sur de Iriquois, 300 m, 23.v.1987, P. Hanson (1♂ USNM); Los Diamantes, Guapiles, 200 m, 20.v.1988, P. Hanson (1♂ USNM); Puntarenas, Parrita playa, 13.i.1989, P. Hanson (1♀ USNM);

**Etymology.**—This species is named after its similarity to *I. gigantea*.

**Host.**—Unknown.

**Distribution.**—Costa Rica.

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## A New Cleptoparasitic *Lasioglossum* (Hymenoptera, Halictidae) from Africa

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**Abstract.**—*Lasioglossum (Dialictus) ereptor* Gibbs, new species, is described and illustrated. The sole known specimen, a female, is from Mount Kilimanjaro, Tanzania. The species has several characteristics typical of cleptoparasitic and socially parasitic Halictidae. A brief summary of the independent cleptoparasitic lineages of *Lasioglossum* is given.

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Cleptoparasitism and social parasitism (for simplicity called ‘parasitism’ hereafter) have arisen multiple times among halictid bees (reviewed in Michener 1978; see also Pauly 1984, 1997; Engel et al. 1997; Biani and Wcislo 2007). The widespread genus *Lasioglossum* Curtis *sensu lato* displays a wide range of behavioural systems (reviewed in Michener 1974, 1990; Packer 1993, Yanega 1997) including multiple parasitic lineages (Table 1; Michener 1978, 2007). Parasitic *Lasioglossum* are known only from eastern North America (*Paralictus* Robertson=*Dialictus* Robertson), central Africa (*Paradialictus* Pauly) and Samoa (*Echthralictus* Perkins and Cheesman) (Michener 2007). Each lineage is believed to be a recent derivative of its non-parasitic host taxon (Michener 1978; Pauly 1984). Halictine host species may be solitary or have eusocial societies (e.g. Packer 1990; Eickwort et al. 1996) which might invalidate the distinction between cleptoparasitism and social parasitism for some parasitic halictines (Biani and Wcislo 2007). A new African species of parasitic *Lasioglossum* believed to be a derivative of the subgenus *Dialictus* (sensu Michener 2007) is described.

### METHODS

The descriptive format and abbreviations follow that of Gibbs and Packer

(2006). Terminology follows that of Michener (2007), Engel (2001) and Harris (1979). The diameter of the median ocellus (OD) is used as a relative measure of hair length. Puncture density is given in relation to interspace size (i) and puncture diameter (d). Flagellomeres and metasomal terga and sterna are abbreviated F, T and S, respectively, followed by the appropriate number.

### RESULTS

#### *Lasioglossum (Dialictus) ereptor* Gibbs, new species Figs 1–3.

**Diagnosis.**—Female. Slender halictine with deep blue metallic reflections on the head and mesosoma; metasoma pale orange; distal wing veins (1rs-m, 2rs-m, 2m-cu) weak; scopa absent, vestiture extremely sparse and entirely pale; mandibles not reaching opposing mandibular base, subapical tooth present; labrum with medial tubercle and apical process; macrosculpture and punctation largely absent.

**Differential Diagnosis.**—Females of *L. ereptor* can be distinguished from other African *Dialictus* (= *Afrodialictus* Pauly) by the absence of scopal hairs and reduced penicillus, basitibial plate and median longitudinal specialized area of T5. Fe-



Table 1. Summary of cleptoparasitic or socially parasitic taxa in the halictine bee genus *Lasioglossum*.

Subgenus	Author	Species	Author	Country	Distribution	Host
<i>Paradialictus</i> = <i>Dialictus</i> <sup>1</sup>	Robertson 1901: 229	<i>cephalotes</i> <i>platyparium</i>	Dalle Torre 1896: 57 Robertson 1895: 117	Canada, USA	ON to NC, west to MN ON to GA, west to LA and MN	? <i>L. (D.) zephyrum</i> <sup>3</sup> ? <i>Dialictus</i>
		<i>michiganense</i> <i>simplex</i> <i>asteris</i> <sup>2</sup>	Mitchell 1960: 448 Robertson 1901: 230 Mitchell 1960: 447	USA	ON to NC	<i>Dialictus</i>
<i>Dialictus</i> <sup>1</sup>	Robertson 1902: 48	<i>ereptor</i>	Gibbs 2008: 74	Canada, USA	MA to NC, west to KS ON to AL, west to KS	<i>L. (D.) versatum</i> <sup>4</sup> <i>L. (D.) imitatum</i> <sup>4</sup>
<i>Echthralictus</i>	Perkins and Cheesman 1928: 14	<i>extraordinarium</i>	Kohl 1908: 306	Tanzania	Mt. Kilimanjaro	? <i>Afrodialictus</i> = <i>Dialictus</i>
<i>Paradialictus</i>	Pauly 1984: 691	<i>latro</i> <i>synavei</i>	Perkins & Cheesman 1928: 23 Pauly 1984: 691	Samoa DR Congo (Zaire)	Samoa Virungas N. P.	? <i>Homalictus</i> ? <i>Afrodialictus</i> = <i>Dialictus</i>

<sup>1</sup> *Dialictus* also contains hundreds of non-parasitic species.  
<sup>2</sup> *L. (D.) asteris* may belong to a distinct lineage from other "*Paradialictus*" (Gibbs, in prep.)  
<sup>3</sup> Parasite collected at nesting site of putative host species which is eusocial.  
<sup>4</sup> Parasite collected inside nest of eusocial host species.

males of *L. ereptor* may be distinguished from the parasitic species *L. (Paradialictus) synavei* Pauly by the metallic colouration and pale abdomen of the former, and the black colouration, enlarged head, elongate mandibles with deep preapical incision and lunate propodeal flange of the latter.

*Description.*—*Female.* Body length: 5.0 mm. Head width: 1.3 mm. Head length: 1.2 mm. Fore wing length: 3.5 mm. Inter-tergular distance: 0.9 mm. OD: 0.01 mm.

**Colouration:** Head and thorax deep metallic blue. Labrum, distal margin of clypeus, basal half of mandible brown, remainder of mandible testaceous, apex red; scape and pedicel dark brown; flagellomeres brown, faintly ferruginous; postgena faintly metallic. Tegula dark brown, infused with ferruginous; wing venation brown, pterostigma and distal veins testaceous; wing dusky throughout; legs brown, tarsi infused with testaceous. Propodeum faintly metallic with purplish tinge. Metasoma pale orange.

**Pubescence:** Sparse and pale throughout. Basal area of labrum with apicolateral bristles; mandibles and distal margin of clypeus with sparse fringe of stiff bristles ( $\geq 3OD$ ). Pronotal lobe posterior margin with dense tomentum; remainder of mesosoma with sparse, erect hairs (2OD), longest along posterior margin of mesoscutellum (3OD); mid femoral and tibial combs present but weak; scopa absent; penicillus reduced; wing setae evenly distributed, brown; erect hairs on posterior surface of propodeum with slightly longer branches than other hairs. Terga with sparse, erect hairs on ventrally reflexed portions and premarginal line, more numerous on T4–T5 dorsal surface (2–3OD), fine setae visible on dorsal surface from certain angles; sterna posterior portions with sparse, faintly sinuate, branched hairs, oriented posteriorly (3–4OD).

**Surface sculpture:** Microsculpture weak throughout. Clypeus and supraclypeal area faintly imbricate, shining, with few more or less uniformly spaced punctures



Fig. 1. Lateral habitus of *Lasioglossum ereptor*, n. sp. A) left side B) right side. Scale bar equals 0.5 mm. Inset: Holotype locality label.

( $i=1-2d$ ), paraclypeal, parasupraclypeal, and upper paraocular areas more densely punctate ( $i=d$ ), remainder of face faintly and closely scabriculous; genal area weakly strigate. Mesoscutum and mesoscutellum faintly imbricate, shining, punctures sparse ( $i=2-4d$ ) and fine, posterior margins of mesoscutum and depressed medial area of mesoscutellum with dense punctation ( $i \leq d$ ); mesepisternum faintly scabriculous, tessellate below, hypoepimeral area imbricate. Propodeum tessellate, faint lon-

gitudinal striae on basal portion of dorsal surface. Metasoma smooth, sculpture very obscure, surface weakly coriarius, terga with sparse ( $i=2-5d$ ), very fine punctures on disc; sterna with piliferous punctures posteriorly.

**Structure:** Head slightly broader than long (1.3 : 1.2); inner orbits nearly parallel (slightly closer below at level of clypeus). Labrum short and broad with basal elevation, distal process present, over half length of remainder of labrum; mandible





Fig. 2. Frontal view of head of *Lasioglossum ereptor*, n. sp. Scale bar equals 0.5 mm.

somewhat enlarged, not reaching opposing mandible base, preapical tooth present. Clypeus broader than long (2.5 : 1.0); clypeal length greater than distance from upper margin of clypeus to lower margin of antennal socket; subantennal sutures faint; supraclypeal area convex, more protuberant than rest of face; median ocellus above upper ocular tangent; distance between orbit and lateral ocellus nearly double distance between lateral ocelli (1.7 : 1.0). Hypostomal carinae subparallel; genal area slightly wider than eye in lateral view, preoccipital carina absent. Antenna rather long, nearly reaching mesoscutellum; scape over 6 times as long as maximum width; pedicel about 1.5 times as long as broad, longer than F1; flagellomeres slightly longer than broad, succeeding flagellomeres each slightly longer and broader than preceding one. Dorsolateral angles of pronotum obtuse; mesoscutum convex with declivous anterior and lateral margins; mesoscutellum with median longitudinal depression; tegula narrow ovoid; 2<sup>nd</sup> and 3<sup>rd</sup> transverse

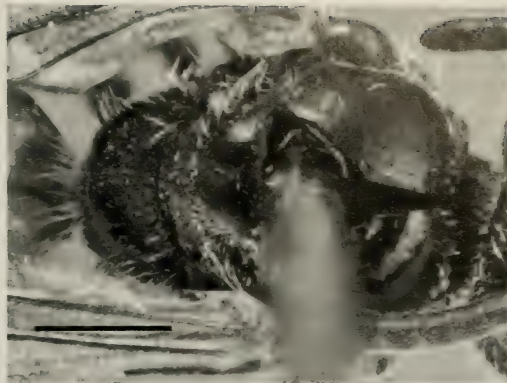


Fig. 3. Dorsal view of mesosoma of *Lasioglossum ereptor*, n. sp. Scale bar equals 0.5 mm.

cubital (1rs-m and 2rs-m) and 2<sup>nd</sup> recurrent (2m-cu) veins and 3<sup>rd</sup> abscissa of vein M weakened; marginal cell with apex pointed on wing margin, pterostigma more than 4 times as long as broad; basitibial plate small, not enclosed by carinae; hind tibial spur pectinate with 4 teeth (not including apex of rachis); metapostnotum long and wide, constituting majority of dorsal propodeal surface, declivous portions of basal area small, rounded onto lateral surface; lateral carina short, reaching less than halfway to dorsal surface. Specialized median area of T5 reduced relative to non-parasitic species. Pygidial plate not visible in holotype.

*Male.* Unknown.

*Etymology.* The specific epithet means 'thief' in Latin and refers to the species' presumed parasitic lifestyle.

*Type Material.* Holotype label reads (typed): "TANZANIA: Mt. Kilimanjaro, Quadrant 2 Giant Senecio zone, area burnt in 1978, Sheffield U. 6.viii.1993 Meru Galdi"

The type specimen is in fair condition except for three missing legs. The left front leg is broken near the base of the femur and the right mid and hind legs are missing beyond the coxae. The pin was placed through the posterior part of the mesoscutum and exits the left mesepisternum near the ventral side. The mesoscutum and mesepisternum have both split as a result.

**Type Depository.** The holotype is currently deposited in the bee collection (PCYU) at York University, Toronto, Canada.

## DISCUSSION

No behavioural data are available for *L. ereptor* but based on several convergent characters common in parasitic halictines, such as the lack of scopa, weak basitibial plate and reduced penicillus, it seems evident that *L. ereptor* is also a cleptoparasite or social parasite. Although many parasitic halictids have thickened cuticles, coarse sculpture and punctation (e.g. many *Sphec. codes* Latreille and *Temnosoma* Smith), which likely function in defence against hosts (Michener 2007), these characteristics are not present in *L. ereptor* nor in the related parasitic groups of *Dialictus* and *Paradialictus*. This lack of coarse sculpturing may be an indication of recent origin or a mode of parasitism that does not require aggressive encounters. The social parasite *L. (D.) asteris* (Mitchell) is capable of entering guarded nests without combat (Wcislo 1997) but nevertheless has an enlarged head and mandibles that could be used for aggressive encounters. Enlarged mandibles are also seen in *Paradialictus* and other parasitic *Dialictus*. The mandibles of *L. ereptor* are larger than those of related non-parasitic species but smaller than those of North American parasitic *Dialictus*.

*Lasioglossum ereptor* is morphologically similar to the *Afrodialictus* group of the large subgenus *Dialictus* (sensu Michener 2007). The genus-group name *Afrodialictus* refers to tropical African members of *Lasioglossum* s. l. with weak, often tessellate sculpturing, widely spaced punctures, an ecarinate and tessellate propodeum and lacking tomentum on the metasomal terga (Pauly 1999). *Afrodialictus* has been classified as a synonym of *Dialictus* (Michener 2007; but see Pauly et al. 2008) and that classification is followed here. *Lasioglossum ereptor* shares the characteristic traits of *Afrodialictus* but may be differentiated by its suite of parasitic characters.

*Lasioglossum (Paradialictus) synavei* is also believed to be a parasitic derivative of *Afrodialictus* (Pauly 1984; Arduser and Michener 1987). Several characters common in cleptoparasites are shared by *L. ereptor* and *L. synavei*. The unique and highly derived mandibles, the lunate flange of the propodeum, large head and black colouration of *L. synavei* are not shared by *L. ereptor* and suggest separate origins of parasitism in these two species. However, both species are of African origin and their type localities are only separated by approximately 900 km on a nearly east-west axis. *Lasioglossum ereptor* may represent a fourth independent lineage of cleptoparasitism in the genus. It is also probable that North American species of parasitic *Dialictus* are not monophyletic (Michener 1978; Gibbs in prep.). Based on the low-level of differentiation from related nest-building species seen in parasitic *Lasioglossum* relative to other parasitic halictines, the origins of parasitic behaviour are relatively recent (Michener 1978; Arduser and Michener 1987). The existence of multiple and recently derived parasitic lineages make *Lasioglossum* an ideal group for studying the origin of cleptoparasitism. Unfortunately, parasitic *Lasioglossum* are not commonly collected. Additional sampling, behavioural studies and systematic treatment of these bees are needed.

In the past, new generic names have been given to parasitic halictines believed to be derived from non-parasitic hosts. For example, the North American parasitic *Dialictus* were formerly called *Paralictus* but are clearly derived from its host *Dialictus* (Danforth 1999; Danforth et al. 2003). Likewise, the parasitic *Echthralictus* and *Paradialictus* are believed to render their presumed hosts, *Homalictus* and *Afrodialictus*, respectively, paraphyletic. Both the names *Echthralictus* and *Paradialictus* have been maintained to simplify the diagnostic characters of their non-parasitic host taxa (Arduser and Michener 1987; Michener 2007). For *Paradialictus*, at least, this seems hardly necessary because



it is likely derived from *Dialictus s. l.* which includes both parasitic and non-parasitic species. *Lasioglossum ereptor* is classified in the subgenus *Dialictus* to prevent an additional genus-group name in the already complex nomenclature of *Lasioglossum s. l.* that would undoubtedly be later placed into synonymy due to parphyly of the host taxon. A robust phylogeny of *Lasioglossum* that includes the parasitic taxa is needed to allow for a more stable classification.

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## A Taxonomic Review of the Genus *Spathius* Nees (Hymenoptera: Braconidae) In North America and Comments on the Biological Control of the Emerald Ash Borer (Coleoptera: Buprestidae)

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**Abstract.**—A review of the braconid genus *Spathius* in North America and comments on several species in the biological control of the Emerald ash borer, *Agrilus planipennis* Fair., are presented. Separate keys to females and males, descriptions, distributions, and biologies are given for the 19 species occurring in North America. One new species, *Spathius leiopleuron* Marsh and Strazanac, **n. sp.**, is described and six new synonymies are proposed as follows: *S. floridanus* Ashmead (= *S. simillimus* Ashmead, **n. syn.**); *S. laflammei* Provancher (= *S. benefactor* Matthews, **n. syn.**); *S. rubidus* (Rossi) (= *S. aphenges* Matthews, **n. syn.**); *S. sequoiae* Ashmead (= *S. canadensis* Ashmead, **n. syn.**, *S. tomoci* Ashmead, **n. syn.**, and *S. claripennis* Ashmead, **n. syn.**).

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In 2002 a new exotic forest pest, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), the emerald ash borer (EAB), was discovered in Michigan and Ontario (Haack et al. 2002; Herms et al. 2004). This pest is native to northeastern China, Korea, Mongolia, Japan, Taiwan, and the Russian Far East. In China, the only recorded hosts are several species of ash (Oleacea: *Fraxinus*) but it has been recorded from species of *Pterocarya* (Juglandaceae) and *Ulmus* (Ulmaceae) in other parts of its native range. In North America, EAB has spread from Michigan and Ontario to Indiana, Missouri, Ohio, Wisconsin, Pennsylvania, West Virginia, Virginia, and Maryland (nursery stock) and has been found to attack all native species of ash.

Shortly after the discovery of EAB in North America, an aggressive control program was established by the USDA Forest Service, Michigan State University, and the Chinese Academy of Forestry. This

included programs to search for natural enemies of EAB both in China and North America. During explorations in China, a species of the braconid wasp genus *Spathius* Nees was discovered which attacked EAB larvae, and preliminary biology and field studies were conducted. This species has subsequently been described as *Spathius agrili* Yang (Yang et al. 2005) and its biology and biocontrol potential are presently being studied in Michigan and China. At the same time, explorations for native natural enemies attacking EAB in North America were started. A number of species of parasitoids were reared in association with EAB, with the Braconidae sent to one of us (PMM) for identification (Bauer et al. 2005). Among the species associated with EAB were specimens of two species of the braconid genus *Spathius*: numerous specimens of *S. floridanus* Ashmead, which occurs throughout eastern North America and has been recorded from several species of *Agrilus* Curtis; and one female and three males of an unde-

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scribed species of *Spathius* (see discussion of this species at end of paper).

The discovery of *S. agrili* in China with its potential for biocontrol of EAB and the subsequent rearing of *S. floridanus* in association with EAB in North America provided an opportunity to study the genus *Spathius* in North America. Matthews (1970) presented a revision of the genus *Spathius* for North America. In this study, we present a revision of Matthew's monograph, including a revised key to species, updated descriptions, synonymies, SEM illustrations of all species, updated distributions and host ranges, and notes on species that might have potential as further parasitoids of EAB. During the course of this study, one new species was discovered, and six new synonyms are proposed.

#### MATERIALS AND METHODS

Several thousand specimens of *Spathius* were borrowed for study from the following institutions: National Museum of Natural History, Washington, DC; American Entomological Institute, Gainesville, FL; Texas A&M University, College Station, TX; California Academy of Sciences, San Francisco, CA; Canadian National Collection, Ottawa, Canada. In addition, specimens were received from biocontrol workers at Michigan State University, and from the USDA Systematic Entomology Laboratory.

Specimens were examined using a Wild M5 stereomicroscope. Scanning electron micrographs were made using the Hitachi S-3500N scanning electron microscope at the Department of Entomology, Kansas State University. Wing photographs were made using a Nikon D100 digital camera mounted on a Leica MZ16 at West Virginia University. The SEM images and wing photographs were enhanced and plates composed using Photoshop (Adobe Systems Incorporated, San Jose, CA) by JSS.

Sculpturing on the body is important in determining species in *Spathius*. Most of the terminology used follows that proposed by Harris (1979). However, some

variations were proposed by Marsh (2002) in his study of the Doryctinae of Costa Rica and the reader is referred to both of these works for definitions of the sculpturing and wing venation terminology. The term precoxal sulcus is used for sternaulus, as proposed by Wharton (2006).

#### Genus *Spathius* Nees

*Spathius* Nees 1818:301.

*Stenophasmus* Smith 1859:169. Synonymized by Szépligeti 1904.

*Euspathius* Foerster 1862:236. Emendation of *Spathius*.

*Pseudospathius* Szépligeti 1902:58. Synonymized by Belokobyl'skij 1992.

*Rhacospathius* Cameron 1905:86. Synonymized by Wilkinson 1931.

**Diagnosis.**—Head cubical, temples broad, occipital carina present and complete; first flagellomere equal to or longer than second; notauli distinct; precoxal sulcus distinct and variously sculptured; metasoma petiolate, first segment narrow at base, more or less parallel sided and suddenly widened at apex, length often several times greater than width; ovipositor at least as long as metasoma beyond petiole, often much longer than entire body; fore tibia with single or double row of 15–50 stout spines along anterior edge; hind coxa with antero-ventral tooth at base; fore wing vein r-m present, vein m-cu meeting vein 2M beyond vein 2RS, first subdiscal cell closed at apex, vein 3CU leaving cell well above middle and often on same line as vein 1CU.

**Distribution.**—Cosmopolitan; especially common in the Old World tropics; rare in Central and South America with one recorded species; 19 species occur in North America.

**Comments.**—In North America, this genus is easily distinguished from all other genera of the subfamily Doryctinae by the petiolate metasoma, and the venation of the fore wing with vein m-cu meeting vein 2M beyond vein 2RS and the closed first subdiscal cell. The subfamily Doryctinae



Figure 1. *Spathius* habitus. (Wharton et al. 1997, used with permission.)

and the genus *Spathius* can be identified using keys provided in Wharton et al. (1997) and Marsh (1997), respectively. In 1973, Matthews and Marsh established the genus *Notiospathius* for the Neotropical species previously included in the genus *Spathius*. Although recent phylogenetic studies (Zaldivar-Riverón et al. 2007, 2008) have shown that the two genera are not closely related, they are similar morphologically and can be distinguished using the keys provided by Marsh (1997, 2002).

Nixon (1943) presented a revision of the Old World *Spathius* in which he separated the species into nearly 50 species groups. Matthews (1970) stated "Although in a few cases the Nearctic species could be construed to fit certain of Nixon's (1943) groups of Old World *Spathius*..., none possess the

exact combination of characteristics of these groups;...". We agree with this statement. Although many of the North American species seem to agree with Nixon's *exarator*-group, most cannot be placed accurately in any of these groups. Matthews did separate the species into what he called natural groupings and gave them group names. However, we have also found these groupings to be difficult to define and, thus, have not used species-groups in this study.

Separate keys to females and males are provided below. Males are always more difficult to identify because usually they are smaller and the characters less distinct. The key to males may be difficult to use and the best way to distinguish males is by association with females in rearings or by DNA analysis.



KEY TO THE NORTH AMERICAN SPECIES OF *SPATHIUS* NEES

Females

1.	Precoxal sulcus with distinct carina along lower margin extending from epicnemial carina to mid-coxal cavity (Figs 4B, 19B) .....	2
—	Precoxal sulcus without a distinct carina along lower margin .....	3
2(1).	Fore wing vein 2RS longer than vein 3RSa (Fig 19F); ovipositor longer than metasoma .....	<i>trifasciatus</i> Riley
—	Fore wing vein 2RS equal in length, or nearly so, to vein 3RSa (Fig 4H); ovipositor shorter than metasoma .....	<i>brunneus</i> Ashmead
3(1).	Eyes small, malar space at least 3/4 eye height, often equal (Figs 2A, 13A, 18A) ....	4
—	Eyes larger, malar space at most 1/2 eye height .....	7
4(3).	Ovipositor at least twice as long as metasoma .....	<i>stigmatus</i> Matthews
—	Ovipositor at most as long as metasoma .....	5
5(4).	Scutellum rugose (Fig 13D); vertex and temple smooth (Figs 13A, B) ...	<i>marshi</i> Matthews
—	Scutellum smooth (Fig 2D); vertex and temples rugulose (Figs. 2A, B) .....	6
6(5).	Maxillary palpus very short, at most equal to eye height .....	<i>brevipalpus</i> Matthews
—	Maxillary palpus longer, usually twice eye height .....	<i>brachyurus</i> Ashmead
7(3).	Petiole long and narrow, at least as long as 1.5 times length of middle femur, usually longer, in side view gently sloping toward base (Figs 5D–E, 7D, 8D–E) .....	8
—	Petiole shorter, never longer than 1.5 length of middle femur, in side view strongly arched at base (Fig 16D) .....	11
8(7).	Scutellum smooth and polished (only male known) .....	<i>longipetiolatus</i> Ashmead
—	Scutellum not smooth, usually weakly acinose or acinose .....	9
9(8).	Metasomal terga 2–4 distinctly and completely sculptured (Fig 5F), lateral margin of terga 2+3 sharp and distinct its entire length; fore wing vein 3CU interstitial and on same line as vein 1CU (Fig 5G) .....	<i>calligaster</i> Matthews
—	Metasomal terga 3 and 4 smooth, lateral margin of terga 2+3 sharp only at base; fore wing vein 3CU not on same line as vein 1CU, thus vein 2CU present (Figs 7F, 8G) .....	10
10(9).	Vertex transversely striate, at least directly behind ocelli (Fig 8A); metasomal terga 2–3 completely sculptured on basal 3/4; hind tarsomere 3 distinctly longer than 5 ...	<i>evansi</i> Matthews
—	Vertex smooth (Fig 7A); metasomal terga 2–3 with sculpture obscured in middle and not covering basal 3/4; hind tarsomere 3 equal or shorter than 5 ..	<i>elegans</i> Matthews
11(7).	Ovipositor shorter than metasoma, usually about equal in length to gaster .....	12
—	Ovipositor equal to or longer than metasoma .....	13
12(11).	Vertex smooth and polished (Fig 16A) .....	<i>rubidus</i> (Rossi)
—	Vertex finely striate (Fig 15A) .....	<i>parvulus</i> Matthews
13(11).	Ovipositor at least as long as entire body, occasionally slightly longer ..	<i>scomes</i> Matthews
—	Ovipositor equal to or slightly longer than metasoma .....	14
14(13).	Vertex and temples distinctly and strongly rugose-acinose, the rugae usually continuing down temple to mandible (Fig 9A); vertex broad, ocellar-occiput distance usually 1.5 times longer than ocellar-ocular distance .....	<i>floridanus</i> Ashmead
—	Vertex and temples at most weakly striate, rugulose or acinose, often entirely smooth, rugae on temples rarely extending to mandibles (Figs 10A, 11A, 12A, 14A, 17A); vertex narrower, ocellar-occiput distance at most 1.2 times longer than ocellar-eye distance, often equal .....	15
15(14).	Forewing weakly infumated and usually without distinct dark transverse bands, occasionally with weak indistinct bands (Fig 17E) .....	<i>sequoiae</i> Ashmead
—	Forewing with distinct dark transverse bands, rarely these bands weakly infumated .....	16
16(15).	Vertex narrow, length (ocellar-occipital distance) equal to or less than ocellar-ocular distance (Fig 10A); outer apical margin of hind tibia with 2–3 small spines (Fig 10E) .....	<i>impus</i> Matthews

- Vertex broader, length greater than ocellar-ocular distance; outer apical margin of hind tibia with 3-6 small spines ..... 17
  - 17(16). Mesopleuron with delicately swirled striae above precoxal sulcus (Fig 14B); vertex more or less evenly weakly strigose (Fig 14A); body color yellow ..... *pallidus* Ashmead
  - Mesopleuron entirely smooth or weakly acinose above precoxal sulcus (Fig 11B, 12B); vertex entirely smooth or weakly strigose anteriorly, usually smooth posteriorly and near eyes (Figs 11A, 12A); body dark honey yellow or brown ..... 18
  - 18(17). Mesopleuron entirely smooth from precoxal sulcus to subalar area (Fig. 12B); vertex entirely smooth (Fig 12A) ..... *leiopleuron* Marsh and Strazanac, new species
  - Mesopleuron weakly acinose or striate, occasionally smooth directly above precoxal sulcus (Fig 11B); vertex weakly striate medially and anteriorly (Fig 11-A) ..... *laflammei* Provancher
- 

## Males

- 1. Precoxal sulcus with distinct carina along lower margin extending from epicnemial carina to mid-coxal cavity ..... 2
- Precoxal sulcus without a distinct carina along lower margin ..... 3
- 2(1). Fore wing vein 2RS longer than vein 3Rsa ..... *trifasciatus* Riley
- Fore wing vein 2RS equal in length, or nearly so, to vein 3Rsa ... *brunneus* Ashmead
- 3(1). Eyes small, malar space at least 3/4 eye height, often equal ..... 4
- Eyes larger, malar space at most 1/2 eye height ..... 7
- 4(3). Hind wing with stigma-like swelling at junction of veins SC+R, r-m and R (Fig. 18H) ..... *stigmatus* Matthews
- Hind wing without such stigma-like swelling ..... 5
- 5(4). Scutellum rugose; vertex and temple smooth ..... *marshi* Matthews
- Scutellum smooth; vertex and temples rugulose ..... 6
- 6(5). Maxillary palpus very short, at most equal to eye height (the unknown male of *brevipalpus* will presumably run here) ..... *brevipalpus* Matthews
- Maxillary palpus longer, usually twice eye height ..... *brachyurus* Ashmead
- 7(3). Petiole long and narrow, at least as long as 1.5 times length of middle femur, usually longer, in side view gently sloping toward base ..... 8
- Petiole shorter, never longer than 1.5 length of middle femur, in side view strongly arched at base ..... 11
- 8(7). Scutellum smooth and polished ..... *longipetiolatus* Ashmead
- Scutellum not smooth, usually weakly acinose or acinose ..... 9
- 9(8). Metasomal terga 2-4 distinctly and completely sculptured, lateral margin of terga 2+3 sharp and distinct its entire length; fore wing vein 3CU interstitial and on same line as vein 1CU ..... *calligaster* Matthews
- Metasomal terga 3 and 4 smooth, lateral margin of terga 2+3 sharp only at base; fore wing vein 3CU not on same line as vein 1CU, thus vein 2CU present ..... 10
- 10(9). Vertex transversely striate, at least directly behind ocelli; metasomal terga 2-3 completely sculptured on basal 3/4; hind tarsomere 3 distinctly longer than 5 ..... *evansi* Matthews
- Vertex smooth; metasomal terga 2-3 with sculpture obscured in middle and not covering basal 3/4; hind tarsomere 3 equal or shorter than 5 ... *elegans* Matthews
- 11(7). Vertex and temple distinctly and strongly acinose to rugose-acinose, the rugae usually continuing down temple to mandible ..... *floridanus* Ashmead
- Vertex and temple at most striate, rugulose or acinose, often entirely smooth, rugae on temple rarely extending to mandibles ..... 12
- 12(11). Fore wings hyaline, without distinct dark bands ..... 13
- Fore wings with distinct dark bands ..... 14



- 13(12). Frons delicately striate ..... *rubidus* (Rossi)  
 – Frons smooth ..... *sequoiae* Ashmead  
 14(12). Vertex nearly entirely striate or strigate ..... *comes* Matthews  
 – Vertex weakly striate, often smooth near eyes and occipital carina or entirely smooth 15  
 15(14). Vertex narrow, ocellar-occipital distance equal or less than ocellar-ocular distance . 16  
 – Vertex broader, ocellar-occipital distance greater than ocellar-ocular distance ..... 17  
 16(15). Sculpture on metasomal terga 2–3 covering at most basal half ..... *impus* Matthews  
 – Sculpture on metasomal terga 2–3 extending beyond basal half ... *parvulus* Matthews  
 17(15). Mesopleuron with delicately swirled striae above precoxal sulcus .. *pallidus* Ashmead  
 – Mesopleuron smooth or weakly acinose above precoxal sulcus ..... 18  
 18(17). Mesopleuron entirely smooth ..... *leiopleuron* Marsh and Strazanac, new species  
 – Mesopleuron weakly acinose above precoxal sulcus ..... *laflammei* Provancher

***Spathius brachyurus* Ashmead**  
 (Figs 2 A–H)

*Rhopalophorus fasciatus* Provancher 1886:129.  
 Preoccupied by Walker 1874.

*Spathius abdominalis* Riley 1890:350. Nomen nudum.

*Spathius brevicaudus* Ashmead 1892:258. Nomen nudum.

*Spathius brachyurus* Ashmead 1893:73; Matthews 1970:26.

*Spathius dignus* Muesebeck and Walkley 1951:169. New name for *fasciatus* Ashmead. Synonymized by Matthews 1970.

*Female*.—*Color*: body varying from light to dark brown; antenna usually with basal flagellomeres light brown and apical ones dark brown; wings lightly dusky, without distinct bands, with infuscated spots below stigma and along vein 1M. *Body size*: 3.0–5.5 mm. *Head*: face rugose or rugose-costate; maxillary palpus about twice eye height; frons rugose; vertex and temple rugulose costate; eyes small, malar space slightly less than eye height, temple about equal to eye width; vertex broad, ocellar-occipital distance slightly greater than ocellar-ocular distance; antenna with 19–25 flagellomeres, those beyond first subcubical, only slightly longer than wide. *Mesosoma*: propleuron rugose; pronotum rugose, costate above fore coxa, propleural groove wide with widely spaced cross carinae; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellar furrow in triangular rugose area with two distinct longitudinal carinae;

scutellum smooth; mesopleuron rugose in subalar area and above middle coxa, central disc acinose; precoxal sulcus distinctly scrobiculate, about 3/4 length of mesopleuron; propodeum rugose, apical lateral corners distinctly produced, median carina and areola distinct, areola with several cross carinae. *Wings*: fore wing vein 2RS nearly as long as vein 3RSa, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m slightly less than 1/2 length of vein 1M. *Legs*: fore tibia with irregular single row of 12–15 spines along anterior edge; hind tibia with 3–4 spines at outer apical lobe; hind coxa with distinct antero-ventral tooth at base. *Metasoma*: petiole arched at base in lateral view, rugose dorsally on basal half, longitudinally carinate on apical half; remainder of terga smooth, with single transverse row of setae at apex of each tergum; ovipositor as long as metasoma.

*Male*.—Essentially as in female; antenna slender, flagellomeres distinctly longer than wide.

*Distribution*.—Quebec south to South Carolina, west to Wisconsin and Texas, California. The California specimens are definitely this species which would indicate *brachyurus* probably occurs throughout North America.

*Biology*.—This species has been recorded attacking *Pissodes strobi* (Peck) and *P. approximatus* Hopkins (Coleoptera: Curculionidae) in pine (Pinaceae; *Pinus*) and

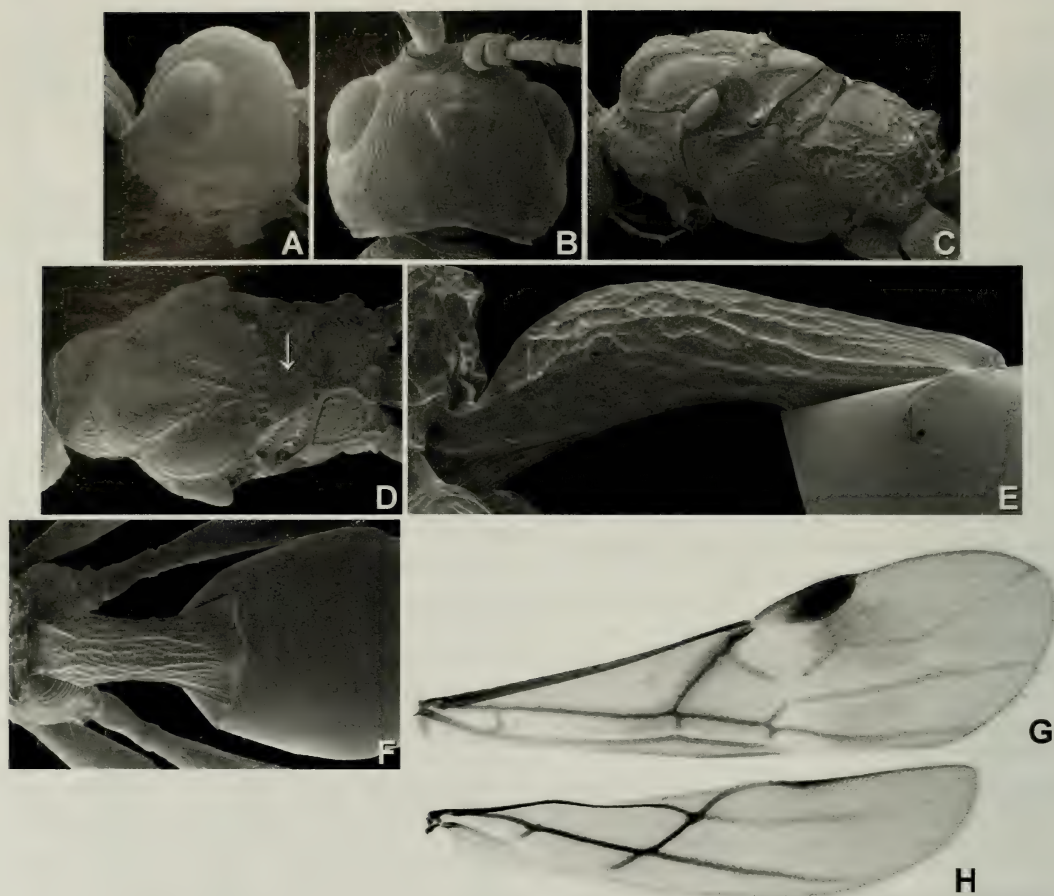


Figure 2. *Spathius brachyurus* Ashmead, female. A, head lateral view; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view with scutellum indicated; E, petiole lateral view; F, petiole and metasoma terga 2+3 dorsal view; G, fore wing; H, hind wing.

*Dryocoetes autographus* (Ratzeburg) (Coleoptera: Scolytidae) in spruce (Pinaceae: *Picea*). The specimens from California are labeled "Galleries of *Steremnius carinatus* and *Hylastes nigrinus* in *Pseudotsuga menziesii*."

**Comments.**—This species and *brevipalpus* are distinctive by the small eye and by the apical lateral corners of the propodeum being protuberant. It can be separated from *brevipalpus* by the longer maxillary palpus and the single transverse row of setae at apex of each metasomal tergum.

*Spathius brevipalpus* Matthews  
(Fig 3A)

*Spathius brevipalpus* Matthews 1970:29.

**Female.**—**Color:** body entirely honey yellow; hind tibia without basal white band; fore wing lightly infuscated, without distinct bands. **Body size:** 3.0–3.5 mm. **Head:** face rugulose, protruding at antennal insertion so that antennae are inserted on distinct frontal shelf; maxillary palpus short, less than eye height; hypostomal carina distinctly protuberant; frons rugose; vertex and temple rugulose-striate; eyes small, malar space about equal to eye height, temple slightly greater than eye width; vertex broad, ocellar-occipital distance greater than ocellar-ocular distance; antenna with 19–20 flagellomeres, those beyond first subcubical, only slightly longer than wide. **Mesosoma:** propleuron ru-



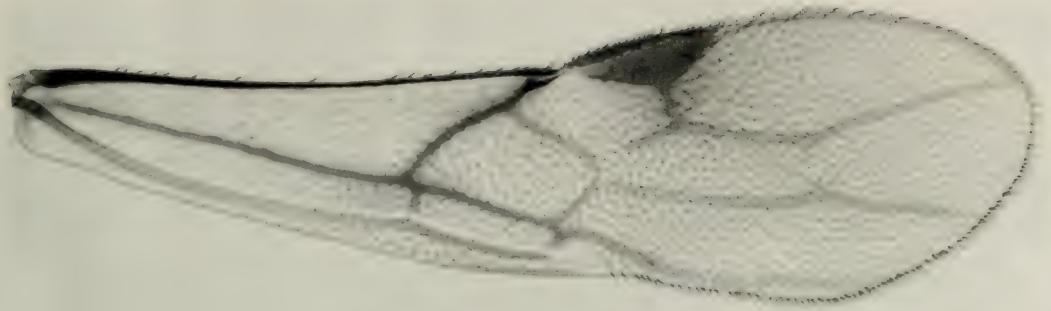


Figure 3. *Spathius brevipalpus* Matthews, female. A, fore wing.

glose; pronotum carinate-rugulose, pronotal groove weakly scrobiculate, nearly smooth; mesoscutal lobes acinose, notauli scrobiculate, meeting before scutellar furrow in shallow rugose area; scutellum smooth, flat; mesopleural disc acinose-rugulose, subalar area coarsely rugose; precoxal sulcus shallow, with weak cross carinae; propodeum with apical-lateral corners strongly produced, rugulose laterally and at basal areas, all propodeal carina distinct, areola with several cross carinae. *Wings*: fore wing vein 2RS about 2/3 length of vein 3RSa, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m about 1/2 length of vein 1M. *Legs*: fore tibia with irregular row of about 15 spines along anterior edge; hind tibia with 3 spines at outer apical rim; hind coxa with distinct antero-ventral tooth at base. *Metasoma*: petiole distinctly arched at base in lateral view, rugulose dorsally at base, longitudinally costate on apical half; all remaining terga smooth and polished, each with two or three transverse rows of long setae; ovipositor about as long as metasoma.

*Male*.—Unknown.

*Distribution*.—Only known specimens are from North Carolina, South Carolina and Texas.

*Biology*.—Unknown. One specimen of the type series from North Carolina was labeled as being reared from "*Pachylobius picivorus*" which has not been confirmed.

*Comments*.—This species and *brachyurus* are distinctive by their small eyes and by the propodeum with apical lateral corners produced; *brevipalpus* can be separated from *brachyurus* by the very short maxillary palpi and the multiple transverse rows of setae on the metasomal terga.

### *Spathius brunneus* Ashmead

(Figs 4 A–I)

*Spathius brunneus* Ashmead 1893:72; Matthews 1970:70.

*Female*.—*Color*: body light honey yellow or orange, metasomal terga beyond third usually brown, apical flagellomeres darker, hind tibia darker with white band on basal 1/5; wings banded, basal 1/3 of stigma yellow. *Body length*: 3.0–5.0 mm. *Head*: face transversely rugulose-striate; frons transversely striate; vertex finely striate anteriorly, diminishing to smooth at occipital carina; temple finely striate to malar mandible; vertex broad, ocellar-occipital distance about twice ocellar-ocular distance; temple about as wide as eye, in dorsal view bulging slightly beyond eye margin; malar space about 1/2 eye height; antenna with 31–34 flagellomeres. *Mesosoma*: propleuron rugulose, propleural flange smooth; pronotum rugulose-striate, pronotal groove weak and often absent; mesoscutal lobes acinose; notauli weakly scrobiculate, meeting before scutellum in shallow triangular rugose area; scutellum

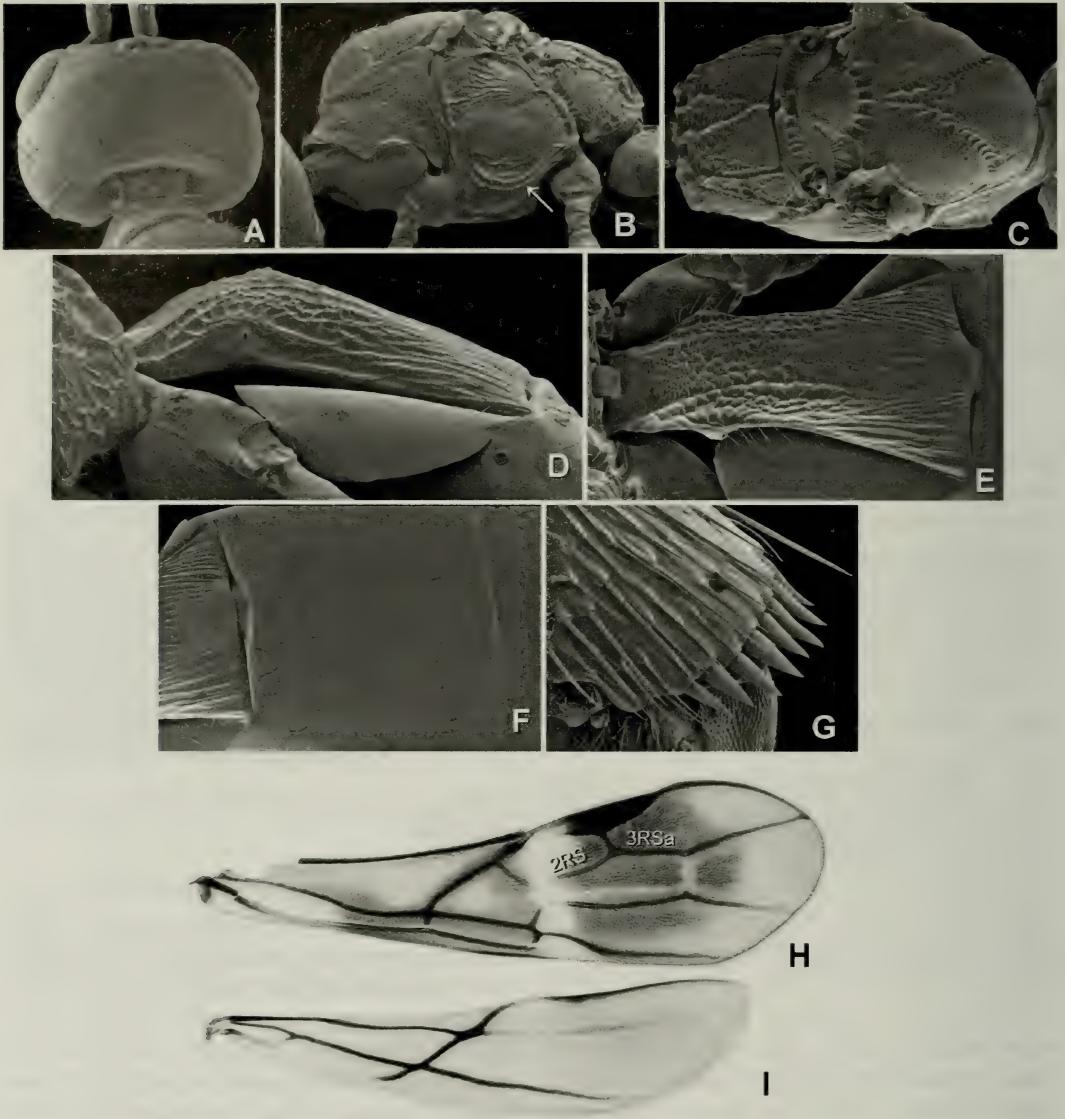


Figure 4. *Spathius brunneus* Ashmead, female. A, head dorsal view; B, mesosoma lateral view with carina along lower margin of sternulus indicated; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, metasoma terga 2+3 dorsal view; G, outer apical margin of hind tibia; H, fore wing with 2RS and 3RSa indicated; I, hind wing.

conical, acinose, scutellar furrow with 6–8 cross carinae; mesopleural disc transversely costate dorsally, weakly acinose above precoxal sulcus, subalar area rugose; precoxal sulcus smooth or with longitudinal carinae, bordered below by strongly curved distinct carina; propodeum acinose laterally, dorsal areas rugulose, carina often indistinct, areola rugulose. *Wings*:

fore wing vein 2RS about equal in length to vein 3RSa, vein 3CU not interstitial with vein 1CU, thus small section of vein 2CU present; hind wing vein r-m less than 1/2 length of vein 1M. *Legs*: fore tibia with 2–3 irregular rows of 30–40 spines along anterior edge; hind tibia with 6–7 spines at outer apical rim; antero-ventral tooth at base of hind coxa weakly pointed. *Meta-*



*soma*: petiole sharply arched in side view at base, rugose on basal 1/2, costate on apical 1/2; second tergum weakly striate-acinose at extreme base, remainder of terga smooth and polished, sometimes with very weak transverse band of punctures anterior to setal bands; ovipositor shorter than metasoma.

*Male*.—Essentially as in female except femora are swollen.

*Distribution*.—The only known specimens are from Maryland, West Virginia and Florida.

*Biology*.—This species has been reared from *Agrilus fallax* Say (Coleoptera: Buprestidae) and *Scolytus muticus* Say (Coleoptera: Scolytidae) infesting *Celtis occidentalis* L. (Ulmaceae).

*Comments*.—This species, along with *trifasciatus*, are distinguished by the precoxal sulcus which is bordered ventrally by a distinct carina. It can be separated from *trifasciatus* by its ovipositor which is shorter than the metasoma (longer than the metasoma in *trifasciatus*), swollen scutellum (flat in *trifasciatus*), the shallower area on the mesoscutum where the notauli meet, and the lighter body color.

***Spathius calligaster* Matthews**  
(Figs 5 A–H)

*Spathius calligaster* Matthews 1970:35.

*Female*.—*Color*: body generally honey yellow to light brown; antenna with scape, pedicel and basal flagellomeres yellow, gradually turning light brown to apex; fore and middle legs including coxae and trochanters yellow, femora and tibiae often darker, hind leg brown except trochanters yellow, hind tibia yellow on apical 1/3 or 1/4; fore wing banded, tegula yellow. *Body size*: 5.5–7.0 mm. *Head*: face transversely costate-rugose; frons transversely costate; vertex striate behind ocellae, smooth near occipital carina; temple smooth except weakly striate near eyes; malar space 1/2 eye height, temple slightly less than eye width; vertex broad, ocellar-ocular dis-

tance slightly less than ocellar-occipital distance; antenna with 25–45 flagellomeres. *Mesosoma*: mesosoma somewhat flattened dorso-ventrally; propleuron rugose; pronotum costate posteriorly, rugose anteriorly, pronotal groove distinctly scrobiculate; mesoscutal lobes coarsely acinose, notauli scrobiculate anteriorly, meeting posteriorly before scutellum in depressed coarsely rugose area; scutellum acinose; mesopleuron longitudinally costate, disc smooth above precoxal sulcus, subalar area rugose, precoxal sulcus distinctly scrobiculate, nearly as long as mesopleuron; propodeum entirely rugose, carinae absent except for short section of median carina. *Wings*: fore wing vein 2RS distinctly curved, vein 2RS about 1/3 length of vein 3RSa, vein 3CU on same line as vein 1CU; hind wing vein r-m about 1/4 length of vein 1M, vein m-cu distinctly basad of vein r-m. *Legs*: fore tibia with irregular row of 15–20 spines along anterior edge; hind tibia without spines at apical lobe; hind coxa elongate, acinose, distinct antero-ventral tooth at base. *Metasoma*: petiole long and slender, about 2/3 length of gaster, evenly sloped to bas in lateral view, nearly entirely rugose dorsally; metasomal terga 2–5 acinose except apical edges smooth; terga 2–3 strongly margined laterally for entire length; ovipositor as long as or longer than entire body.

*Male*.—Essentially as in female.

*Distribution*.—Quebec south to South Carolina, west to Illinois and Ohio.

*Biology*.—The only reliable rearing record is from *Melasis pectinicornis* Melsh. (Coleoptera: Eucnemidae).

*Comments*.—This species is distinctive by its coarsely sculptured gaster, especially terga 2–5, and the absence of spines at the apical lobe of the hind tibia.

***Spathius comes* Matthews**  
(Figs 6 A–C)

*Spathius comes* Matthews 1970:59.

*Female*.—*Color*: entire body honey yellow or light brown; legs often lighter, trochan-

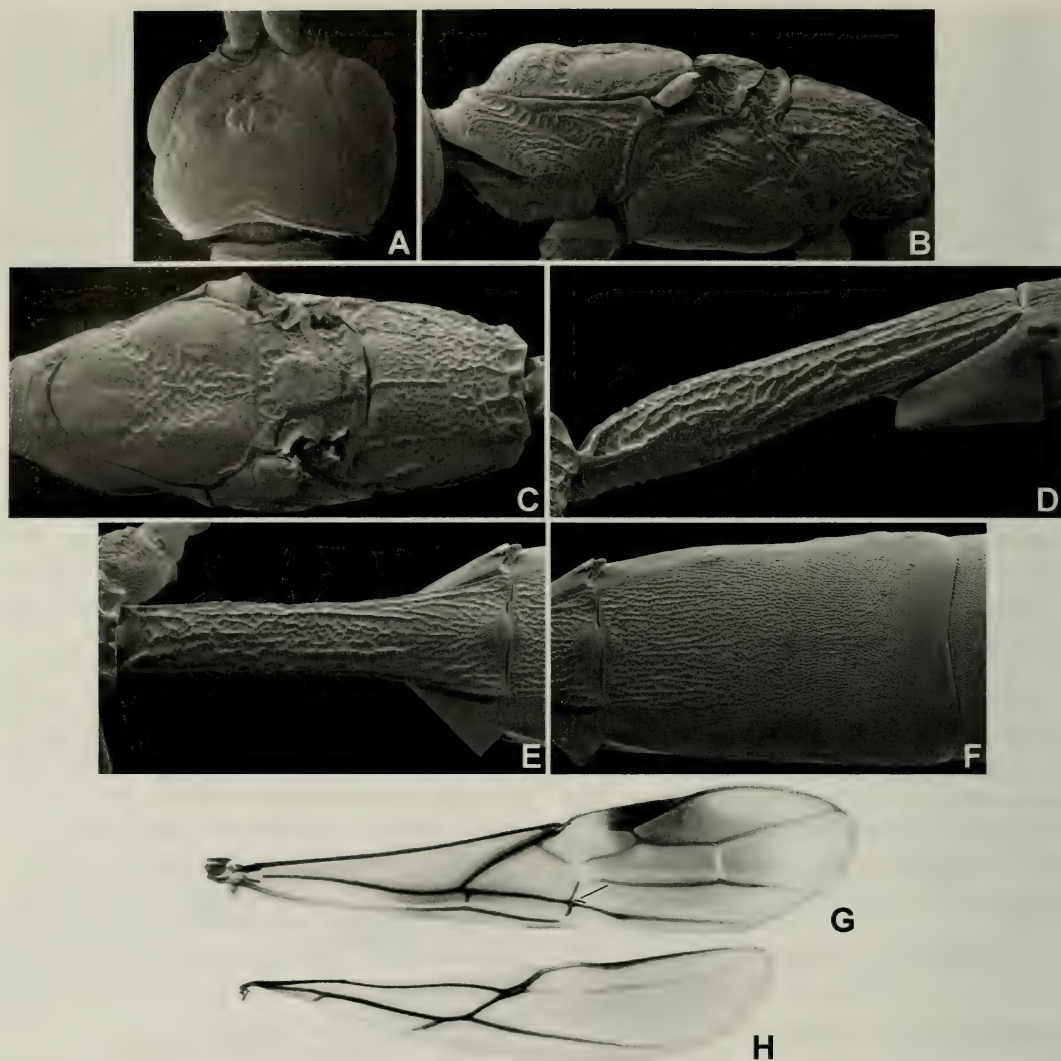


Figure 5. *Spathius calligaster* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, metasoma terga 2+3 dorsal view; G, fore wing with interstitial 2CU vein indicated; H, hind wing.

ters usually yellow; antennae yellow at base, becoming light brown to apex; wings banded, basal 1/3 of stigma yellow. *Body size*: 2.5–5.0 mm. *Head*: face transversely striate-rugulose; frons transversely striate; vertex striate, becoming striate-acinose laterally; temple acinose; vertex broad, ocellar-ocular distance about 2/3 ocellar-occipital distance; malar space 1/2 eye height; antenna with 26–38 flagellomeres. *Mesosoma*: propleuron rugulose, propleural flange broad and smooth along posterior

border; pronotum rugose above and below pronotal groove which is scrobiculate except costate posteriorly; mesoscutal lobes acinose, notauli scrobiculate anteriorly, meeting before scutellum in triangular rugose area; scutellum acinose; propodeum acinose on basal lateral areas and laterally, rugose dorso-laterally, along median carina and at apex, carinae and areola not distinct. *Wings*: fore wing vein 2RS equal in length to vein 3RSa, vein 3CU not on same line as vein 1CU, short vein 2CU





Figure 6. *Spathius comes* Matthews, female. A, head dorsal view; B, fore wing; C, hind wing.

present; hind wing vein r-m about  $2/5$  length of vein 1M. *Legs*: fore tibia with two irregular rows of 15–30 spines along anterior edge; hind tibia with three spines at outer apical lobe; hind coxa acinose, with blunt small antero-ventral tooth at base. *Metasoma*: petiole distinctly arched at base in lateral view, rugose dorsally except costate at extreme apex; terga 2–3 acinose on basal  $1/2$ , remainder of terga smooth; ovipositor usually as long as entire body, occasionally slightly longer.

*Male*.—Essentially as in female.

*Distribution*.—Nova Scotia and Quebec south to Maryland, west to Wisconsin and Ohio.

*Biology*.—Reared from *Chrysobothris pusilla* Cast. (Coleoptera: Cerambycidae) in spruce and *Melanophila fulvoguttata* (Harr.) (Coleoptera: Buprestidae) in hemlock (Pinaceae: *Tsuga*).

*Comments*.—This species is similar to *floridanus* because of the vertex sculpturing but is distinguished by the ovipositor which is as long as or longer than the entire body.

### *Spathius elegans* Matthews (Figs 7 A–G)

*Spathius elegans* Matthews 1970:39.

*Female*.—*Color*: head and mesosoma usually light brown, occasionally honey yellow, propodeum honey yellow; petiole honey yellow, gaster light brown, apex of third tergum often lighter; antenna yellow,

becoming light brown apically; legs honey yellow, fore and mid coxae and trochanters and hind trochanters yellow, hind tibia with white or yellow band on basal  $1/4$ – $1/5$ ; wings banded, basal  $1/3$  of stigma yellow. *Body size*: 3.5–7.0 mm. *Head*: face and frons transversely striate; vertex smooth; temple smooth, occasionally weakly acinose behind eye; malar space  $1/2$  eye height; temple about equal to eye width; vertex broad, ocellar-occiput distance about 1.5 times ocellar-ocular distance; antenna with 30–40 flagellomeres. *Mesosoma*: propleuron rugose; pronotum rugose, propleural groove scrobiculate-rugose; mesoscutal lobes acinose, notauli scrobiculate, meeting posteriorly in excavated triangular rugose area with two converging distinct longitudinal carinae; scutellum acinose; mesopleural disc acinose-rugulose, subalar area coarsely rugose, precoxal sulcus scrobiculate, about  $2/3$  length of mesopleuron; propodeum acinose dorsally and laterally, rugose dorso-laterally, median carina and areola distinct. *Wings*: fore wing vein 2RS equal to or sometimes slightly longer than vein 3RSa, vein 3CU nearly on same line as 1CU; hind wing vein r-m less than  $1/2$  length of vein 1M. *Legs*: fore tibia with irregular double row of 25–50 spines along anterior edge; hind tibia with 3–5 spines on outer apical lobe; hind tarsomere 3 slightly shorter than tarsomere 5; hind coxa acinose, with small but distinct antero-ventral tooth at base. *Metasoma*: petiole long and

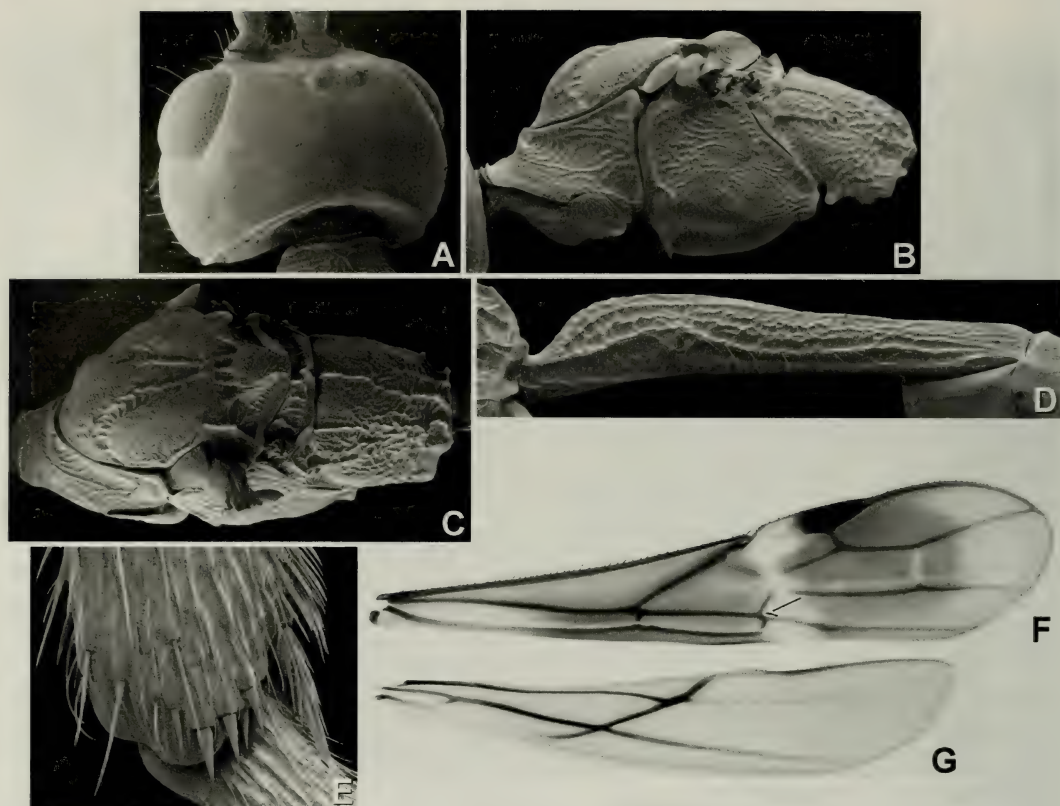


Figure 7. *Spathius elegans* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

slender, about  $3/4$  length of mesosoma, dorsally rugulose; second metasomal tergum acinose, third tergum weakly acinose laterally and usually smooth medially; remainder of terga smooth; ovipositor about as long as entire body.

*Male*.—Essentially as in female.

*Distribution*.—This is perhaps the most widely collected species and occurs throughout North America.

*Biology*.—In spite of the many specimens studied, there are no accurate host records. The species has been reared from maple (Aceraceae: *Acer*), beech (Betulaceae: *Betula*) and hickory (Juglandaceae: *Carya*) and has been associated with powderpost wood infested with *Hadrobregmus* (Coleoptera: Anobiidae).

*Comments*.—This species is similar to *evansi* but is distinguished by the smooth vertex, less sculptured metasomal terga 2–

3, and the third hind tarsomere shorter than the fifth tarsomere.

### *Spathius evansi* Matthews (Figs 8 A–H)

*Spathius evansi* Matthews 1970:42.

*Female*.—*Color*: body generally entirely honey yellow or light brown; fore and mid coxae and trochanters and hind trochanters lighter yellow, hind tibia with yellow band on basal  $1/4$ ; antenna becoming light brown apically; wings banded, stigma yellow on basal  $1/3$ . *Body size*: 3.5–9.0 mm. *Head*: face and frons transversely costate; vertex transversely costate or striate at least behind ocelli and near eyes, often on entire vertex; temple smooth, occasionally weakly striate near mandible; malar space slightly less than  $1/2$  eye height; temple equal to eye width; antenna



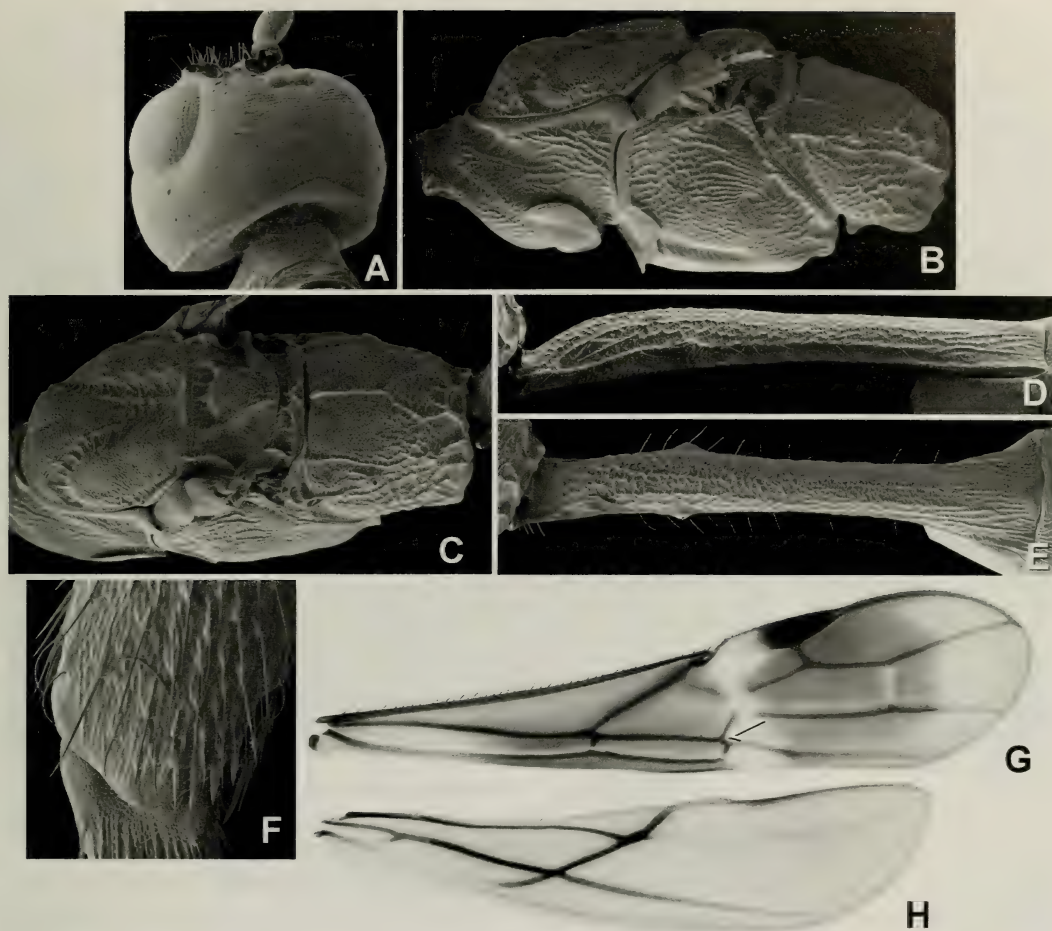


Figure 8. *Spathius evansi* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, outer apical margin of hind tibia; G, fore wing with 2CU indicated; H, hind wing.

with 35–50 flagellomeres; temple broad, ocell-occiput distance about 1.5 times ocellar-ocular distance. *Mesosoma*: propleuron acinose posteriorly, rugulose anteriorly; pronotum rugulose medially and dorsally, acinose ventrally and over pronotal collar, pronotal groove distinctly scrobiculate, obscured posteriorly; mesoscutal lobes acinose, notauli scrobiculate, meeting posteriorly in deeply excavated triangular rugulose area; scutellum acinose; mesopleural disc acinose above precoxal sulcus, transversely costate dorsally and posteriorly, subalar area often rugulose; precoxal sulcus distinctly scrobiculate, about 2/3 length of mesopleuron; propodeum aci-

nose apically and laterally, rugulose apically and along dorsal lateral edge, basal carina and areola usually distinct, often weakly indicated. *Wings*: fore wing vein 2RS about as long as vein 3RSa, vein 3CU not on same line as vein 1CU so that short section of vein 2CU present; hind wing vein r-m less than half length of vein 1M. *Legs*: fore tibia with irregular double row of 25–35 spines along anterior edge; hind tibia with 2–5 spines at outer apical lobe; hind tarsomere 3 usually distinctly longer than tarsomere 5; hind coxa acinose, with distinct sharply pointed antero-ventral tooth at base. *Meta-soma*: petiole long and narrow, nearly as long as mesosoma, rugulose-acinose dor-

sally; terga 2–3 distinctly and evenly acinose on basal 3/4, apical 1/4 smooth; remainder of terga smooth; ovipositor longer than entire body, usually twice as long as fore wing.

*Male*.—Essentially as in female.

*Distribution*.—Quebec south to Florida, west to Wyoming and New Mexico. Probably occurs throughout North America.

*Biology*.—No hosts have been recorded and we have not seen any reared specimens.

*Comments*.—This species is very similar to *elegans* but can be distinguished by its striate vertex (smooth in *elegans*), the metasomal terga 2–3 being sculptured on basal 3/4 (*elegans* has a smooth area medially), and third hind tarsomere being longer than the fifth (shorter in *elegans*).

***Spathius floridanus* Ashmead**  
(Figs 9 A–I)

*Spathius floridanus* Ashmead 1893:71; Matthews 1970:75.

*Spathius simillimus* Ashmead 1893:73; Matthews 1970:72. **New synonymy.**

*Female*.—*Color*: body honey yellow or light brown, apical terga of metasoma often brown; hind tibia with white band at basal 1/6; antenna yellow basally, becoming light brown to apex; wings distinctly banded. *Body size*: 1.5–4.5 mm. *Head*: face transversely rugulose-costate; vertex transversely costate-acinose, often becoming acinose near and behind eye; frons rugulose or transversely rugulose-costate; temple and malar space acinose; vertex broad, ocellar-ocular distance 2/3 ocellar-occipital distance; temple bulging slight beyond eye margin in lateral view; malar space about 1/2 eye height; antenna with 25–40 flagellomeres. *Mesosoma*: propleuron rugulose, occasionally acinose on propleural flange; pronotum longitudinally costate behind and above pronotal groove, before groove often acinose or costate-acinose; pronotal groove distinctly scrobiculate; mesoscutal lobes acinose; notauli strongly scrobiculate anteriorly, meeting posteriorly in triangu-

lar depressed rugose area; scutellum acinose; mesopleural disc strongly longitudinally costate dorsally, costae becoming weaker near precoxal sulcus and often acinose just above precoxal sulcus, which is scrobiculate; subalar area rugose; propodeum rugulose with distinct basal carinae and areola, basal lateral areas often acinose, lateral area often acinose. *Wings*: fore wing vein 2RS equal to or slightly shorter than vein 3RSa, vein 3CU not on same line as vein 1CU, thus small segment of vein 2CU present; hind wing vein r-m less than half length of vein 1M. *Legs*: fore tibia with irregular single or double row of 15–25 spines along anterior edge; hind tibia with 2–6 spines on outer apical lobe; hind coxa with small but distinct antero-ventral tooth at base. *Metasoma*: petiole arched at base in lateral view, dorsally rugose at base, longitudinally costate at apex; gastral tergum 2 weakly acinose or strigate at base, often nearly entirely smooth, remainder of gastral terga smooth; terga 4–6 occasionally with a weakly defined transverse punctate band anterior to row of setae; ovipositor equal to or slightly longer than metasoma.

*Male*.—Essentially as in female.

*Distribution*.—New Brunswick south to Florida, west to Ontario, Wisconsin and Texas.

*Biology*.—Recorded hosts are: *Agrilus anxius* Gory, *A. bilineatus* (Weber), *Chrysobothris femorata* (Oliv.) (Coleoptera: Buprestidae); *Magdalis olya* (Herbst) (Coleoptera: Curculionidae); *Phymatodes aereum* (Newman), *Xylotrechus colonus* (F.) (Coleoptera: Cerambycidae). In addition, we have seen specimens of *floridanus* reared from galleries of *Agrilus planipennis*, the emerald ash borer, from Michigan.

*Comments*.—Matthews (1970) based his separation of *simillimus* from *floridanus* primarily on the presence of a transverse punctate band on gastral terga 4–6 anterior to the transverse row of setae. Our examination of several hundred specimens has shown a wide variation of this band from distinct to absent. This variation, including



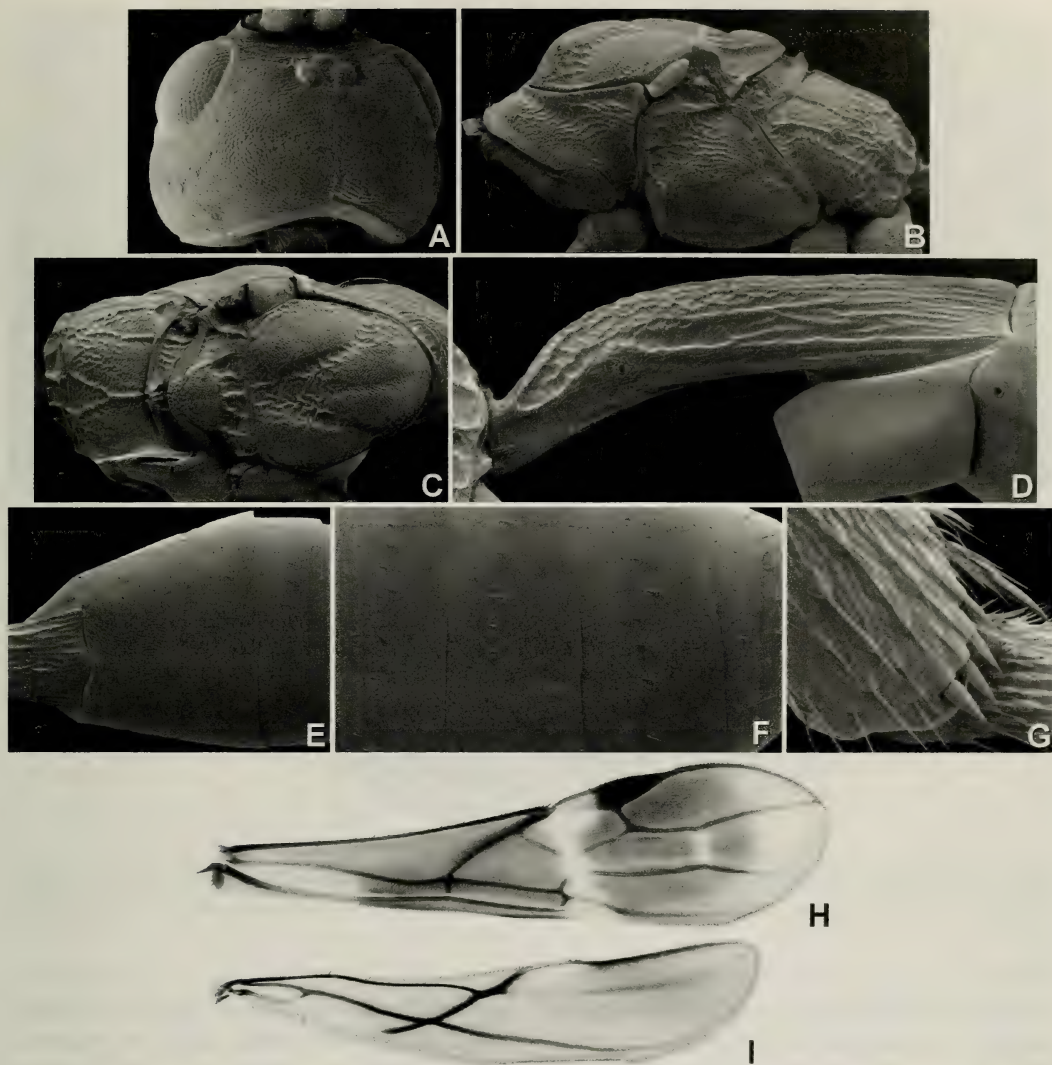


Figure 9. *Spathius floridanus* Ashmead, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, metasoma terga 2+3, and 4 dorsal view; F, metasoma terga 4, 5, 6, and 7 dorsal view; G, outer apical margin of hind tibia; H, fore wing; I, hind wing.

the wide overlap in number of spines at the apical lobe of the hind tibia and the wide variation in sculpture of the mesopleural disc, has convinced us that *simillimus* and *floridanus* are the same species. The name *floridanus* is chosen because of its page preference in Ashmead's original publication (Ashmead 1893).

***Spathius impus* Matthews**  
(Figs 10 A–G)

*Spathius impus* Matthews 1970:56.

**Female.**—**Color:** body honey yellow, apical half of metasoma usually light brown, legs lighter yellow; wings banded; antenna yellow basally, gradually becoming light brown to apex. **Body size:** 1.5–3.5 mm. **Head:** face weakly rugulose-striate; frons striate; vertex strigate; temple smooth, occasionally weakly acinose near occipital carina; malar space  $1/2$  eye height; vertex narrow, ocellar-ocular distance about equal to ocellar-occipital distance; antenna with 20–30 flagellomeres. **Mesosoma:** propleuron

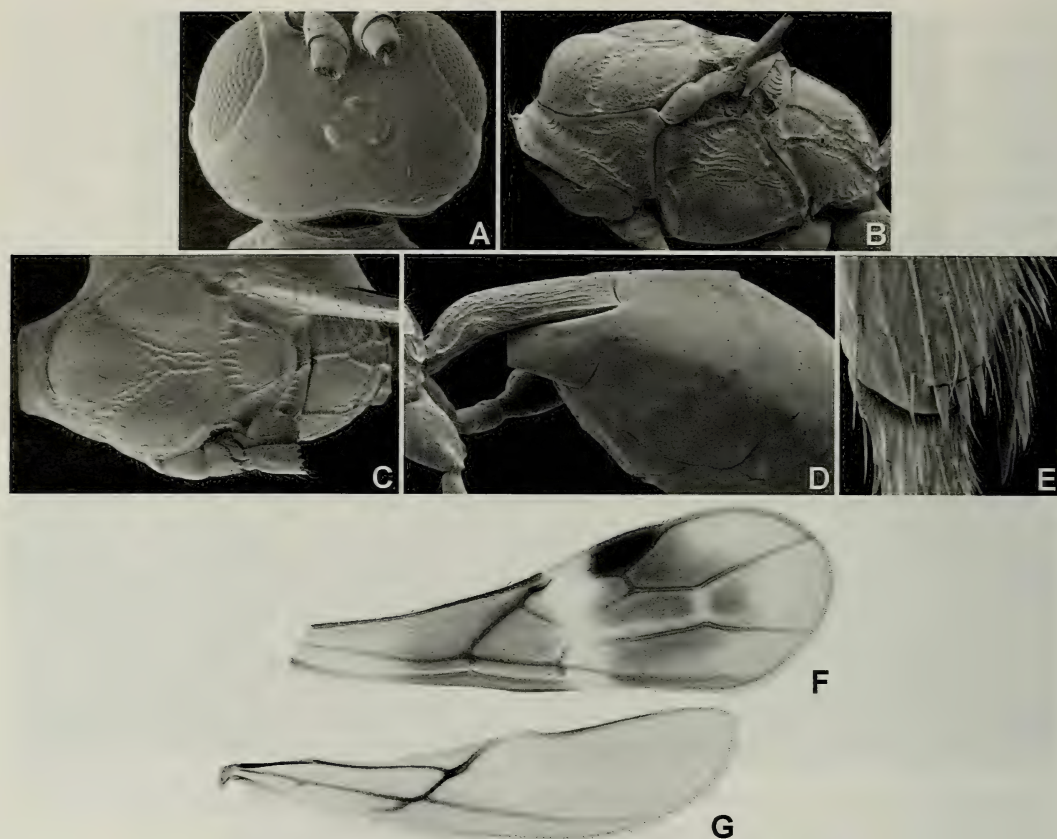


Figure 10. *Spathius impus* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole and metasoma lateral view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

rugulose; pronotum rugulose, pronotal groove scrobiculate but weakly or not at all impressed; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in narrow triangular rugose area, often with two distinct short longitudinal carinae; scutellum acinose; mesopleural disc acinose, becoming longitudinally costulate dorsally, subalar area costate; precoxal sulcus scrobiculate, only weakly impressed; propodeum distinctly acinose dorsally and laterally, areola and basal carina distinct. *Wings*: fore wing vein 2RS slightly longer than vein 3RSa, vein 3CU nearly on same line as vein 1CU, occasionally very short segment of vein 2CU present; hind wing vein r-m about 1/3 length vein 1M. *Legs*: fore tibia with

irregular row of about 15 spines along anterior edge; hind tibia with 3–4 spines at outer apical lobe. *Metasoma*: petiole arched at base in lateral view, dorsally rugose on basal half, costate on apical half; second tergum weakly acinose on basal half, remainder smooth; remainder of terga smooth; ovipositor equal to or slightly longer than metasoma.

*Male*.—Essentially as in female.

*Distribution*.—Quebec south to Florida, west to Michigan and Louisiana.

*Biology*.—Reared from *Phloeosinus canadensis* Swaine and *P. dentatus* (Say) (Coleoptera: Scolytidae) in red cedar (Cupressaceae: *Juniperus*).

*Comments*.—This species is similar to *parvulus* but is distinguished by the ovi-



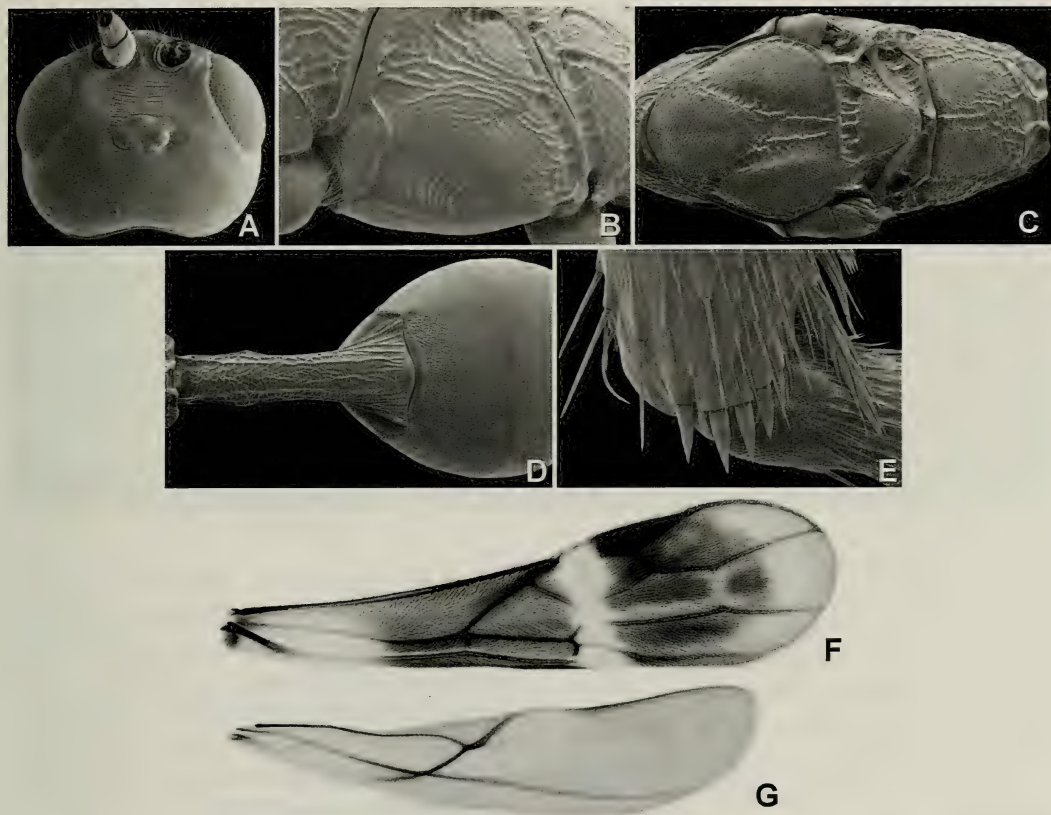


Figure 11. *Spathius laflammei* Provancher, female. A, head dorsal view; B, mesopleuron; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

positor being as long as or longer than the metasoma (shorter than the metasoma in *parvulus*); it is also similar to *pallidus* but is distinguished by the narrower vertex (broader in *pallidus*).

***Spathius laflammei* Provancher**  
(Figs 11 A–G)

*Spathius laflammei* Provancher 1880: 164; Matthews 1970:64.

*Spathius benefactor* Matthews 1970:61. **New synonymy.**

**Female.**—**Color:** body dark honey yellow to brown, petiole and base of gaster often lighter; antenna yellow, becoming darker apically; legs honey yellow, trochanters often lighter, hind tibia with basal 1/4–1/5 yellow or white; wings banded. **Body**

**length:** 2.5–6.00 mm. **Head:** face transversely striate; frons delicately transversely striate; vertex weakly transversely striate medially, becoming smooth near eyes and occiput, occasionally entirely smooth; temple smooth dorsally, often weakly acinose near malar space; vertex broad, ocellar-ocular distance about 2/3 ocellar-occipital distance; malar space slightly less than 1/2 eye height; antenna with 30–45 flagellomeres. **Mesosoma:** propleuron rugulose; pronotum rugulose dorsally and ventrally, porcate along posterior border at end of pronotal groove which is strongly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in depressed triangular rugose area, often with two distinct longitudinal carinae; scutellum acinose; mesopleuron

smooth or weakly acinose directly above precoxal sulcus, longitudinally costate dorsally and along posterior border, subalar area rugose; precoxal sulcus distinctly scrobiculate; propodeum rugulose dorsally, rugose laterally and apically, basal carina and areola usually distinct but often obscured, areola usually narrow and much longer than wide. *Wings*: fore wing vein 3RSa equal to or slightly longer than vein 2RS, vein 3CU not on same line as vein 1CU, short section of vein 2CU present; hind wing vein r-m about 1/3 length of vein 1M. *Legs*: fore tibia with two irregular rows of 20–40 spines along anterior edge; hind tibia with 3–8 spines on outer apical lobe. *Metasoma*: petiole arched at base in lateral view, shorter than gaster, rugose basally and becoming longitudinally costate-rugose apically; terga 2–3 acinose on basal 1/3–1/2, remainder smooth; remainder of terga smooth and polished; ovipositor slightly longer than metasoma.

*Male*.—Essentially as in female.

*Distribution*.—Occurs throughout North America.

*Biology*.—As mentioned by Matthews (1970), this species has been studied extensively under the name *canadensis* and he stated that all references to *Spathius* reared from elm (Ulmaceae: *Ulmus*) actually refer to *benefactor*. The following hosts have been recorded for *benefactor* and *laflammei*: *Hylurgopinus rufipes* (Eichh.), *Leperisinus aculeatus* (Say), *Scolytus multistriatus* (Marsham) and *S. rugulosus* Ratz. (Coleoptera: Scolytidae); *Magdalis armicollis* (Say), *M. barbata* (Say), *M. inconspicua* Horn, *M. olyra* (Coleoptera: Curculionidae); *Saperda tridentata* Oliv. (Coleoptera: Cerambycidae).

*Comments*.—We have seen most of the specimens that Matthews studied for his descriptions of *benefactor* and *laflammei* and have concluded they represent one highly variable species. There is considerable overlap in the ranges of characters mentioned by Matthews, such as number of teeth on the outer lobe of the hind tibia and number of antennomeres, and it was

difficult to place most specimens in one or the other species. Matthews even hinted at this in his description of *benefactor* by stating "Larger individuals are superficially similar to *laflammei*..." We found this to be true with all size specimens and thus have considered *benefactor* to be a synonym of *laflammei*. This species is close to *pallidus* but can be distinguished by the smooth or weakly acinose mesopleuron above the precoxal sulcus (swirled striae in *pallidus*) and the nearly smooth vertex (weakly but evenly striate in *pallidus*).

***Spathius leiopleuron* Marsh and  
Strazanac, new species**  
(Figs 12 A–G)

*Female*.—*Color*: head light brown, antennae yellow at base, gradually turning brown to apex; mesosoma light brown, pronotum dark brown anteriorly, mesoscutal lobes often dark brown, metascutum dark brown, mesopleuron occasionally darker dorsally, propodeum occasionally dark brown; petiole light brown, remainder of metasomal terga dark brown; wings distinctly banded, veins dark brown, basal fourth of stigma bright yellow; all coxae and trochanters honey yellow, femora and tibiae brown, tibiae with bright yellow band at base, tarsi light brown. *Body size*: 3.0–4.5 mm. *Head*: face transversely costate; frons distinctly depressed, weakly transversely striate; vertex and temple entirely smooth and polished; malar space 1/3 eye height; temple slightly less than eye width; vertex broad, ocellar-occipital distance slightly greater than ocellar-ocular distance; antenna with 24–30 flagellomeres. *Mesosoma*: propleuron transversely striate; pronotum rugose-striate below pronotal groove, costate above, pronotal groove wide and distinctly scrobiculate; mesoscutal lobes acinose, notauli deeply scrobiculate, meeting posteriorly in deeply depressed triangular rugose area with two distinct longitudinal carinae; scutellum weakly acinose, occasionally smooth; me-



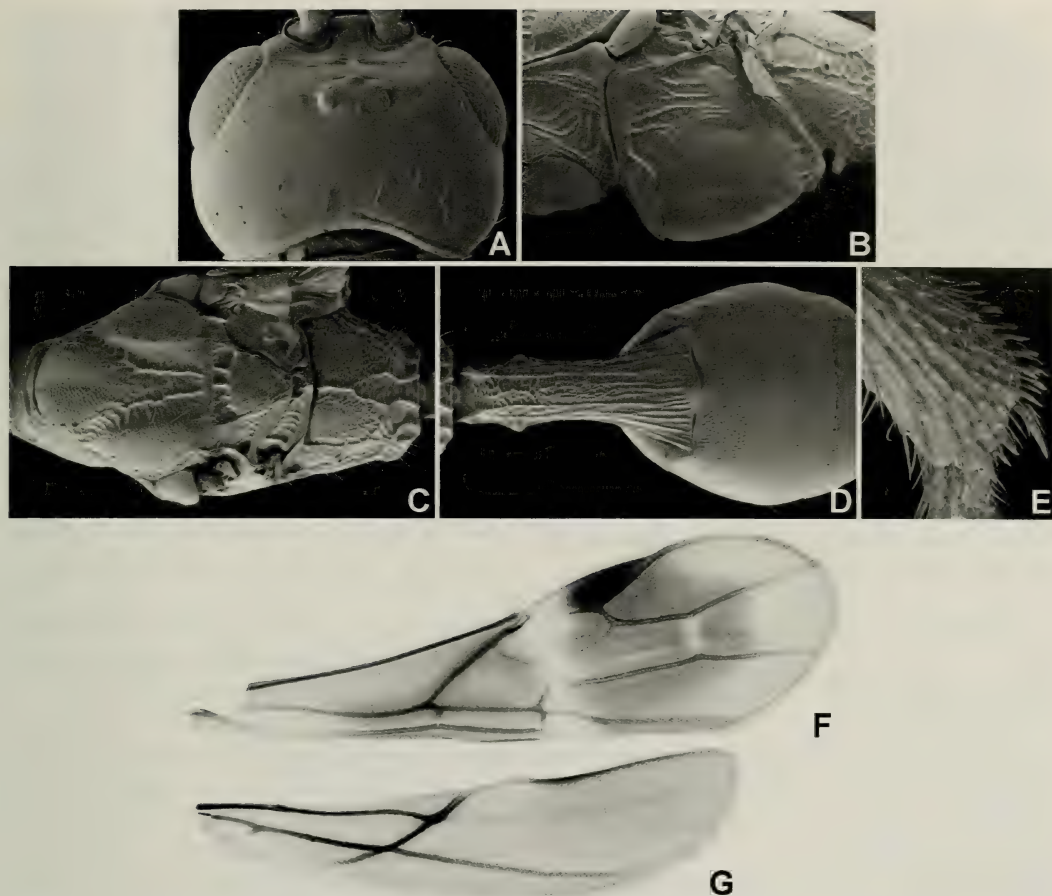


Figure 12. *Spathius leiopleuron* Marsh and Strazanac, new species, female. A, head dorsal view; B, mesopleuron; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

sopleuron entirely smooth except for longitudinally carinate subalar area, precoxal sulcus weakly scrobiculate; propodeum rugulose with distinct median carina, areola and lateral carinae, areola transversely costate. *Wings*: fore wing veins 3RSa and 2RS equal in length, vein 3CU not on same line as vein 1CU, short section of vein 2 CU present; hind wing vein r-m  $1/3$  length of vein 1M. *Legs*: fore tibia with 2–3 irregular rows of 25–30 spines along anterior edge; hind tibia with 3–4 spines at outer apical lobe; hind coxa with distinct antero-ventral tooth at base. *Metasoma*: petiole arched at base in lateral view, coarsely longitudinally rugose-costate dorsally; second tergum entirely acinose; third

tergum punctate across basal  $1/3$ , remainder smooth; remainder of terga smooth, terga 4–6 occasionally with transverse punctate band at base; ovipositor slightly longer than metasoma.

*Male*.—Essentially as in female; body size 2.0–3.5 mm.

*Holotype female*.—USA: Maryland, Montgomery Co., 4 mi. southwest Ashton,  $39^{\circ}06'36\text{N}$ ,  $77^{\circ}01'30\text{W}$ , iii.04 em. iv–v 2004, M. Gates; Reared from dead *Prunus* infested with Coleoptera. Deposited in U. S. National Museum of Natural History, Washington, DC.

*Paratypes*.—8 females, 12 males, same data as holotype; 1 female, same locality as holotype, 19.viii.03, Gates/Hevel, on dead

*Prunus* (Rosaceae) infested with scolytids/cerambycids; 1 female, same locality as holotype, 24.viii.03, E. Grissell, on dead *Prunus* infested with scolytids/cerambycids. Deposited in U. S. National Museum of Natural History, Washington, DC, and Department of Plant and Soil Sciences/Entomology, West Virginia University.

**Biology.**—Unknown. Type series indicates host is a wood boring beetle, probably a scolytid or cerambycid.

**Comments.**—This species is characterized by the entirely smooth mesopleuron which will distinguish it from all other species.

**Etymology.**—The species name is from the Greek *leios*, meaning smooth, and the Greek *pleura*, meaning side, in reference to the smooth mesopleuron.

### *Spathius longipetiolatus* Ashmead

*Spathius longipetiolatus* Ashmead 1893:70; Matthews 1970:38.

Matthews (1970:38) prepared a complete description of the two male specimens available at that time. No further specimens, including females, have been discovered and the reader is referred to Matthews for the description. This species is distinctive by the smooth scutellum, elongate petiole, and strongly striate vertex.

### *Spathius marshi* Matthews

(Figs 13 A–H)

*Spathius marshi* Matthews 1970:30.

**Female.**—**Color:** head honey yellow, malar space often lighter; scape. Pedicel and basal flagellomeres honey yellow, flagellum becoming brown to apex; mesosoma honey yellow to light brown; metasoma honey yellow to light brown, apical terga often lighter; legs light brown, hind tibia without basal yellow band; wings lightly dusky without distinct bands, stigma brown with indistinct basal yellow spot. **Body size:** 2.5–3.5 mm. **Head:** face, including clypeus, transversely costate; frons transversely costate; vertex and temple smooth;

eye small, malar space equal to eye height; temple slightly wider than eye width; vertex broad, ocellar-occiput distance about equal to ocellar-ocular distance; antenna with 22–24 flagellomeres. **Mesosoma:** propleuron rugose with several distinct carinae; pronotum rugose, propleural groove distinct, very broad and deep, broadly scrobiculate; mesoscutal lobe rugose, acinose medially; notauli wide and deeply scrobiculate; scutellum rugose, scutellar furrow with median distinct cross carina and often smaller and less distinct carinae laterally; mesopleural disc smooth, subalar area rugose; precoxal sulcus wide and deep, smooth, divided into two or three foveae by one or two cross carinae, extending to mid coxa as distinct longitudinal carina; propodeum rugose, with distinct basal carinae, areola and lateral carinae, apical lateral areas slightly protuberant. **Wings:** fore wing vein 2RS about 2/3 length of vein 3RSa, vein 3CU nearly on same line as vein 1CU; hind wing vein r-m about 1/4 length of vein 1M. **Legs:** fore tibia with irregular row of 20–25 spines along anterior edge; hind tibia with three spines at outer apical rim; hind coxa with distinct antero-ventral tooth at base. **Metasoma:** petiole distinctly arched at base in lateral view, rugose dorsally on basal half, apical half longitudinally carinate; remainder of terga smooth; ovipositor slightly longer than metasoma.

**Male.**—Essentially as in female; precoxal sulcus often without cross carinae.

**Distribution.**—Quebec south to South Carolina, west to Wisconsin and Kansas.

**Biology.**—Unknown.

**Comments.**—This species is easily distinguished from the other North American species by its rugose scutellum and mesoscutum, by the small eyes, and by the unique shape of the precoxal sulcus.

### *Spathius pallidus* Ashmead

(Figs 14 A–D)

*Spathius pallidus* Ashmead 1893: 74; Matthews 1970:53.



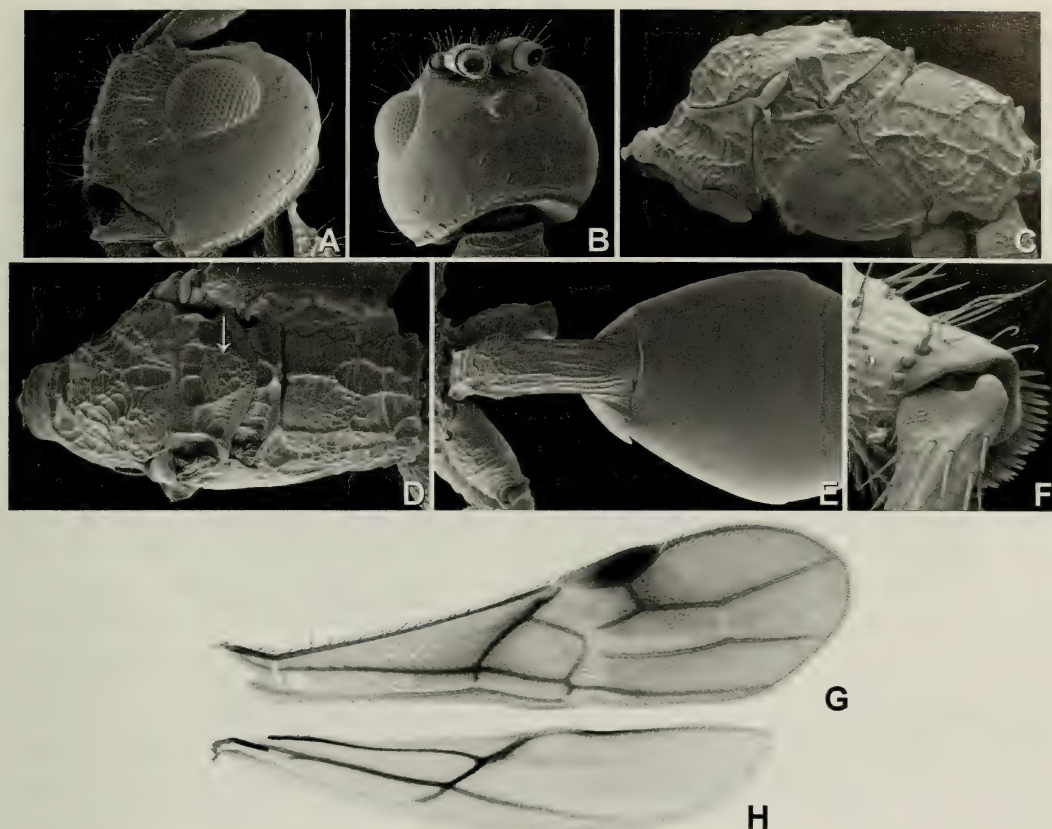


Figure 13. *Spathius marshi* Matthews, female. A, head lateral view; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view; E, petiole and metasoma terga 2+3 dorsal view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing.

**Female.**—**Color:** body generally light honey yellow, apical segments of metasoma often darker; antenna yellow, gradually darkening toward apex; trochanters of all legs usually yellow, hind tibia with yellow band on basal 1/3; wings banded. **Body size:** 2.0–3.0 mm. **Head:** face transversely striate-rugulose; frons transversely striate; vertex transversely striate, becoming acinose or smooth near eye; temple smooth along eye, occasionally acinose near occipital carina; malar space slightly less than eye height; vertex somewhat broad, ocellar-ocular distance slightly shorter than ocell-occiput distance; antenna with 25–35 flagellomeres. **Mesosoma:** propleuron rugulose except flange usually smooth; pronotum striate or striate-rugulose above groove, acinose below, pronotal groove

indistinctly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in narrow triangular rugose area; scutellum acinose; mesopleuron with delicately swirled striae above precoxal sulcus, subalar area porcate; precoxal sulcus scrobiculate; propodeum acinose or acinose-rugulose dorsally and laterally, median carina and areola distinct but occasionally weakly indicated. **Wings:** fore wing vein 3RSa nearly equal in length to vein 2RS, vein 3CU not on same line as 1CU, thus small section of vein 2CU present; hind wing vein r-m slightly more than 1/3 length of vein 1M. **Legs:** fore tibia with irregular double row of 18–25 spines along anterior edge; outer apical lobe of hind tibia with 3–5 spines; hind coxa with small but distinct antero-ventral tooth at

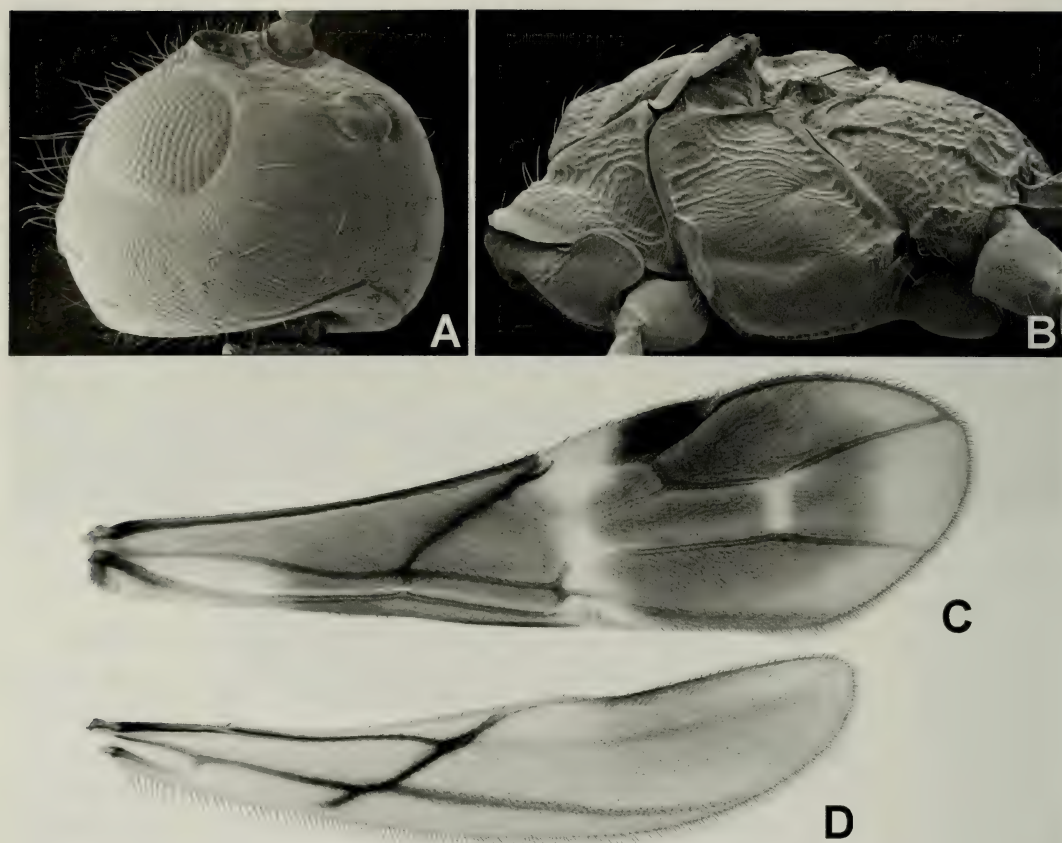


Figure 14. *Spathius pallidus* Ashmead, female. A, head dorsolateral view; B, mesosoma lateral view; C, fore wing; D, hind wing.

base. *Metasoma*: petiole strongly arched at base in lateral view, rugose dorsally at base, longitudinally striate at apex; metasomal terga 2–3 acinose on basal 1/3, occasionally acinose-striate, remainder smooth; remainder of terga smooth; ovipositor slightly longer than metasoma.

*Male*.—Essentially as in female.

*Distribution*.—Ontario and Massachusetts south to Georgia, west to Montana and Texas. We have also seen specimens from Oregon and British Columbia which are apparently this species, indicating the distribution is probably throughout North America.

*Biology*.—This species has been recorded from the: *Dendroctonus frontalis* Zimm., *Ips avulsus* (Eichh.), *I. grandicollis* (Eichh.) (Coleoptera: Scolytidae); *Pissodes approximatus*

Hopk., *Phloeosinus dentatus*, *P. nemorensis* Germ. (Coleoptera: Curculionidae).

*Comments*.—This species is characterized by the delicately swirled striae on the mesopleuron.

#### *Spathius parvulus* Matthews (Figs 15 A–E)

*Spathius parvulus* Matthews 1970:55.

*Female*.—*Color*: body entirely yellow-brown to honey yellow; antenna yellow at base, gradually darkening to brown at apex; wings banded, stigma with white spot on basal 1/4; hind tibia with white band at basal 1/5. *Body size*: 2.5–3.5 mm. *Head*: face transversely striate-rugulose; frons weakly transversely striate; vertex weakly transversely striate, the striae often



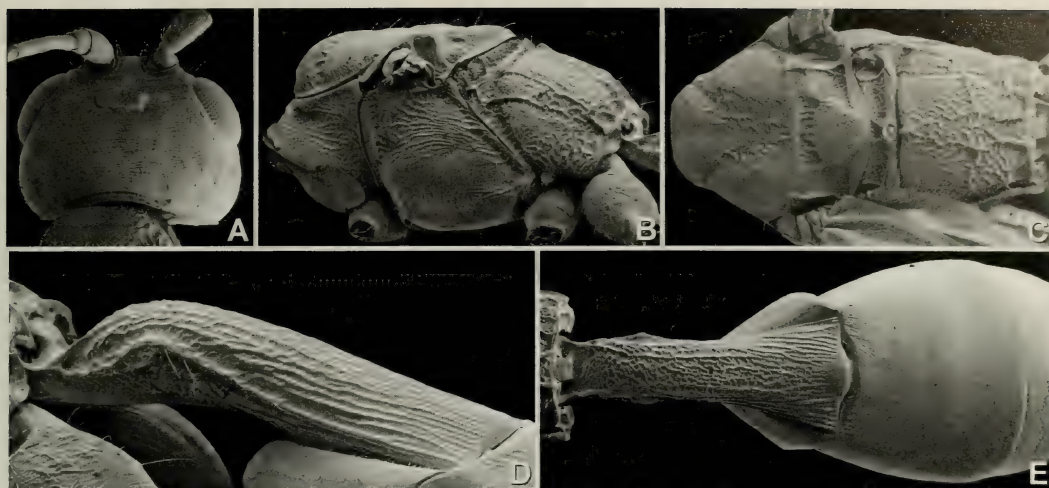


Figure 15. *Spathius parvulus* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma terga 2+3 dorsal view.

curved toward ocelli; temple usually smooth; malar space about  $1/3$  eye height; temple less than eye width; vertex narrow, ocellar-ocular distance equal to ocellar-occipital distance; antenna with 21–29 flagellomeres. *Mesosoma*: propleuron rugulose; pronotum rugose dorsally and ventrally, pronotal groove distinctly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellum in narrow triangular rugose area with two short longitudinal carinae evident; scutellum acinose; mesopleural disc delicately transversely striate, often smooth above precoxal sulcus, subalar area rugose; precoxal sulcus distinctly scrobiculate; propodeum with basal carina and areola distinct, basal lateral area acinose, lateral areas rugulose. *Wings*: fore wing vein 2RS about as long as vein 3RSa, vein 3CU not on same line as vein 1CU; hind wing vein r-m less than  $1/2$  length of vein 1M. *Legs*: fore tibia with single row of 15–20 spines along anterior edge; outer apical lobe of hind tibia with 3 spines; hind coxa with small distinct antero-ventral tooth at base. *Metasoma*: petiole strongly arched at base in lateral view, dorsally rugose on basal half, longitudinally rugose-carinate on apical half; terga 2–3 acinose on basal  $2/3$ , remainder

of terga smooth; ovipositor about as long as gaster.

*Male*.—Essentially as in female.

*Distribution*.—In the original description, Matthews states that the species occurs in New Mexico, Colorado and South Dakota. He also had specimens tentatively placed in *parvulus* from the eastern U. S. We have seen these specimens and others in the National Museum collection and they agree with the description. Thus, *parvulus* probably occurs throughout North America.

*Biology*.—The type series from New Mexico was reared from *Ips* species in ponderosa pine (Pinaceae: *Pinus ponderosa* C. Lawson). A few specimens from Massachusetts were labeled as being reared from *Pissodes strobi*.

*Comments*.—This species is similar to *rubidus* with their short ovipositor, but *parvulus* differs in its striate vertex. The narrow vertex is also similar to *impus* but *parvulus* has a much shorter ovipositor.

### *Spathius rubidus* (Rossi) (Figs 16 A–G)

*Ichneumon rubidus* Rossi 1794:110.

*Spathius rubidus* (Rossi): Nees 1834:14; Nixon, 1943:200; Belokobyl'skij 1998:107.

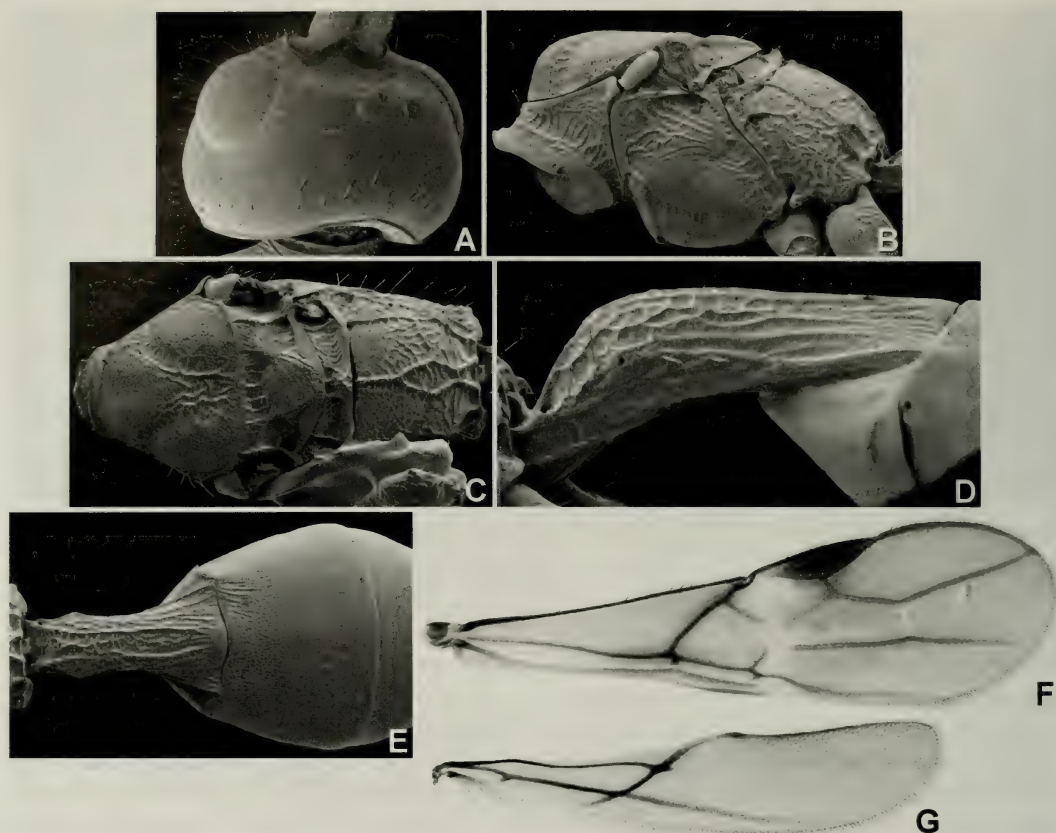


Figure 16. *Spathius rubidus* (Rossi), female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma terga 2+3 dorsal view; F, fore wing; G, hind wing.

*Spathius aphenges* Matthews 1970:51. **New synonymy.**

*Female*.—*Color*: body light brown to brown; legs yellow; antenna yellow, flagellum gradually darkening to brown at apex; wings not distinctly banded, with darker areas below stigma and in first discal and first subdiscal cells, stigma brown with basal 1/4 yellow. *Body size*: 2.5–3.5 mm. *Head*: face finely transversely striate; frons broadly impressed, transversely striate; vertex and temple smooth; malar space about 1/2 eye height; vertex broad, ocellar-ocular distance 3/4 ocellar-occiput distance; antenna with 23–29 flagellomeres. *Mesosoma*: propleuron rugulose; pronotum rugose above and below propleural groove which is wide, distinctly scrobiculate and extends to posterior border of pronotum;

mesoscutal lobes acinose; notauli scrobiculate, meeting before scutellum in slightly depressed triangular rugose area with two distinct converging longitudinal carinae; scutellum acinose; mesopleural disc smooth, subalar area distinctly rugose; precoxal sulcus scrobiculate; propodeum rugulose, lateral carinae distinct, median carina and areola distinct. *Wings*: fore wing veins 2RS and 3RSa about equal in length, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m slightly more than 1/3 length of vein 1M. *Legs*: fore tibia with single row of 10–20 spines along anterior edge; outer apical lobe of hind tibia with 5 spines; hind coxa weakly acinose, with distinct antero-ventral tooth at base. *Metasoma*: petiole strongly arched basally in lateral view, rugose dorsally on basal 2/3,



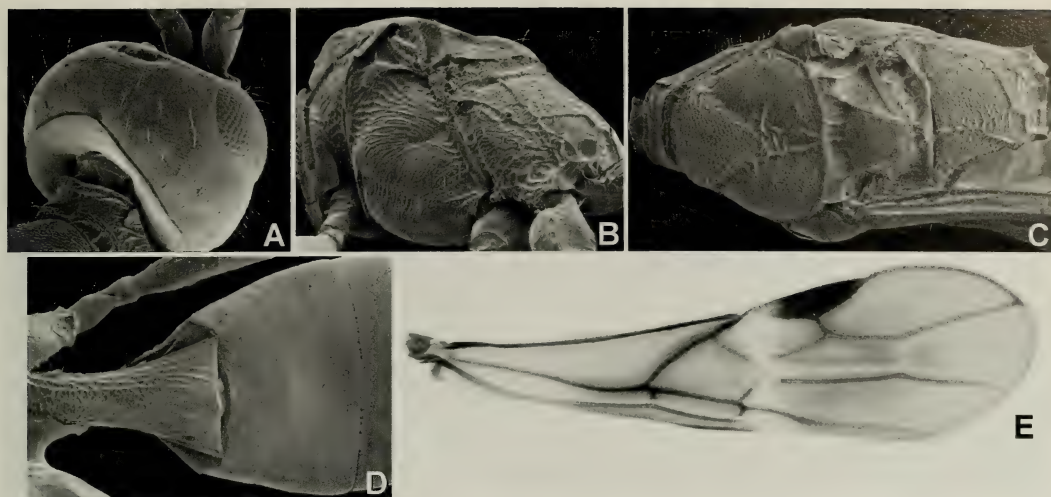


Figure 17. *Spathius sequoiae* Ashmead, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, fore wing.

apical 1/3 longitudinally costate; metasomal terga 2–3 acinose, more weakly so on terga 3 and with posterior edge smooth; remainder of terga smooth; ovipositor shorter than metasoma, usually about equal in length to gaster.

*Male*.—Essentially as in female.

*Distribution*.—Yukon Territory south to Texas, west to British Columbia and California; Europe.

*Biology*.—This species has been reared from a wide variety of scolytids and cerambycids in Europe. In North America it has been reared from *Conophthorus coniperda* (Schwarz), *Ips latidens* (Lec.), *Phloeotribus lecontei* Schedl, and *Scolytus abietis* Blkm. (Coleoptera: Scolytidae).

*Comments*.—We have seen authentically identified specimens of *Spathius rubidus* in the Natural History Museum, London, and there is no question that *aphenges* is the same species. *Spathius rubidus* is distinctive by its short and arched petiole and short ovipositor; it is similar to *parvulus* from which it is distinguished by its smooth vertex.

***Spathius sequoiae* Ashmead**  
(Figs 17 A–E)

*Spathius sequoiae* Ashmead (1888) 1889:625; Matthews 1970:44.

*Spathius canadensis* Ashmead 1891:2; Matthews 1970:47. **New synonymy.**

*Spathius clavipennis* [sic] Ashmead 1892:257. *Nomen nudum.*

*Spathius californicus* Ashmead 1893:70. Synonymized by Matthews 1970:44.

*Spathius tomici* Ashmead 1893:71. Synonymized with *canadensis* by Matthews 1970:48. **New synonymy.**

*Spathius claripennis* Ashmead 1893:72. Synonymized with *canadensis* by Matthews 1970:47.

**New synonymy.**

*Spathius brunneri* Viereck 1912:627. Synonymized by Matthews 1970:44.

*Female*.—*Color*: body honey yellow to light brown, base of gaster and apex of petiole usually darker; legs often lighter than body; antenna yellow basally becoming brown at apex; wings nearly hyaline, often with indistinct weak bands. *Body size*: 2.5–4.0 mm. *Head*: face transversely striate-rugulose; frons transversely strigate, sometimes nearly smooth; vertex weakly transversely strigate medially, often nearly smooth; temple smooth or weakly acinose; malar space about 1/2 eye height; vertex narrow, ocellar-ocular distance about equal to ocellar-occipital distance; antenna with 22–32 flagellomeres. *Mesosoma*: propleuron rugulose; pronotum rugulose, pronotal

groove weakly indicated, weakly scrobiculate; mesoscutal lobes acinose, notauli scrobiculate and meeting at scutellum in narrow triangular rugose area, often with two distinct longitudinal carinae; scutellum acinose; mesopleural disc transversely striate, often acinose or smooth directly above precoxal sulcus, subalar area transversely costate; precoxal sulcus slightly more than half length of mesopleuron, weakly scrobiculate; propodeum rugose, areola distinct and often long and narrow, basal carina often short. *Wings*: fore wing vein 2RS equal to or slightly longer than vein 3RSa, vein 3CU not on same line as vein 1CU, thus short segment of vein 2CU present, vein 1cu-a beyond vein 1M; hind wing vein r-m slightly less than 1/2 length of vein 1M. *Legs*: fore tibia with single or irregular double and occasionally triple row of 10–30 spines along anterior edge; hind tibia with 2–5 spines at outer apical lobe. *Metasoma*: petiole strongly arched at base in lateral view, rugose dorsally on basal half, costate on apical half; second metasomal tergum acinose or weakly strigate on basal 2/3, occasionally nearly smooth, remainder of terga smooth; ovipositor equal to or slightly longer than metasoma.

*Male*.—Essentially as in female.

*Distribution*.—Widespread in Northern North America, from Maine to higher elevations in North Carolina, west to Alaska and California.

*Biology*.—This species attacks a wide variety of scolytids in coniferous trees. Matthews considered most host records from elm for *canadensis*, as he defined the species, to belong to his new species *benefactor*, which is considered a synonym of *laflammei* in the present study (Matthews 1970). Recorded hosts are as follows: *Alniphagus aspericollis* Lec., *Cryphalus pubescens* Hopk., *Dendroctonus obes* (Mann.), *D. pseudotsugae* Hopk., *Dryocoetes autographus* (Ratz.), *Ips pini* (Say), *Lechriops californicus* (Lec.), *Orthotomicus caelatus* (Eichh.), *Pityophthorus balsameus* Blkm., *Phloeosinus*

*punctatus* Lec., *P. sequoiae* Hopk., *Pissodes* sp., *Polygraphus rufipennis* (Kirby), *Pseudohylesinus nebulosus* (Lec.), *P. sericeus* (Mann.), *Scolytus laricis* Blkm., *S. piceae* (Swaine), *S. tsugae* Swaine, *S. unispinosus* Lec., *S. ventralis* Lec. (Coleoptera: Scolytidae).

*Comments*.—Matthews (1970) retained *sequoiae* and *canadensis* as separate species but considered the separation as tentative. We have seen all the specimens that Matthews studied and several more series and consider the species to be one fairly variable species. This species is similar to *rubidus* but can be separated by the ovipositor which is equal to or longer than the metasoma (in *rubidus* it is shorter than the metasoma and usually not longer than the gaster).

### *Spathius stigmatus* Matthews

(Figs 18 A–H)

*Spathius stigmatus* Matthews 1970:32.

*Female*.—*Color*: head, mesosoma, and petiole light brown, metasoma beyond petiole dark brown; legs light brown, hind tibia white on basal 1/4; antenna honey yellow, apical 6–8 flagellomeres light brown to brown; fore wing mostly darkly infumated except for subhyaline band at apex and across middle from base of stigma, stigma yellow on basal 1/3. *Body length*: 3.5–5.0 mm. *Head*: eyes small, malar space 3/4–4/5 eye height; face transversely striate; frons transversely striate; vertex finely striate, smooth around ocelli; temple finely striate; vertex broad, ocellar-occipital distance about 1.5 times ocellar-ocular distance; temple broader than eye width; antenna with 16–19 flagellomeres, those beyond third less than twice as long as wide, all flagellomeres with a circle of 4 long erect setae on apical rim. *Mesosoma*: propleuron, including flange, smooth; pronotum longitudinally carinate, pronotal groove scrobiculate anteriorly and over pronotal collar, absent posteriorly; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellar furrow in triangular



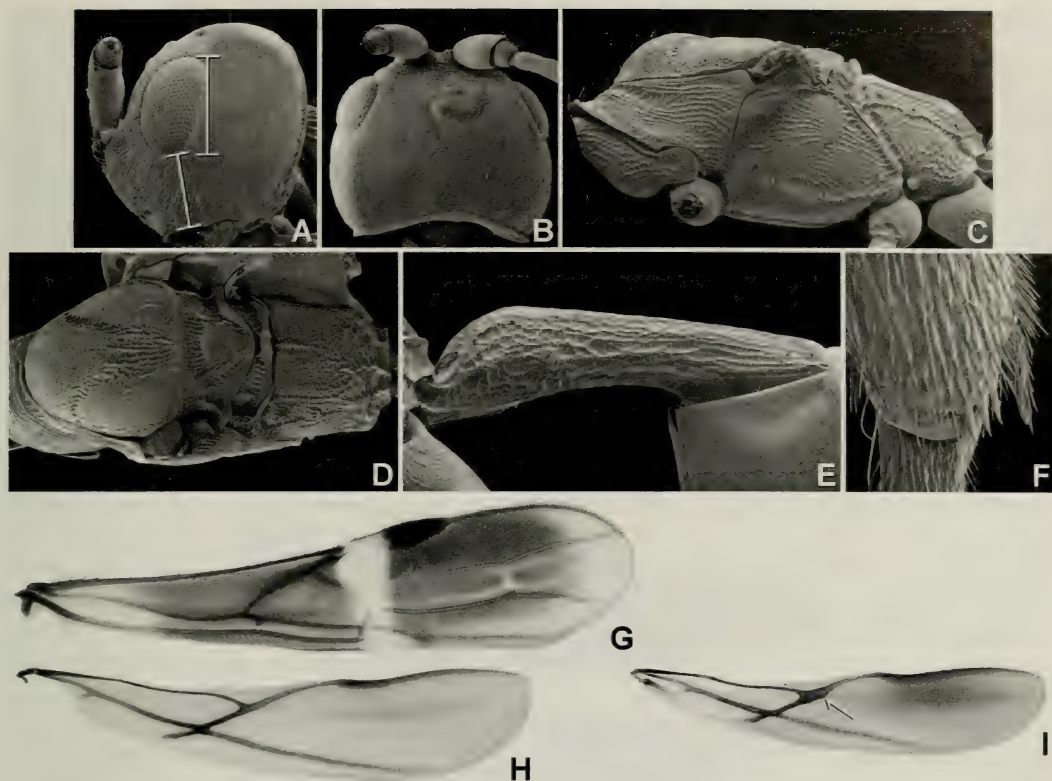


Figure 18. *Spathius stigmatus* Matthews, female. A, head lateral view with eye height and malar space measurement indicated; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view; E, petiole lateral view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing. Male, I, hind wing with stigma-like swelling indicated.

carinate-rugulose area; scutellum acinose, scutellar furrow with 7–8 evenly spaced cross carinae; mesopleural disc longitudinally carinate, subalar area rugose; precoxal sulcus shallow, distinctly scrobiculate; propodeum acinose dorsally, becoming rugose apically, acinose laterally, carinae and areola obscured, lateral carinae distinct. *Wings*: fore wing vein 2RS shorter than vein 3RSa, vein 3CU on same line as vein 1CU; hind wing vein r-m about 1/2 length of vein 1M. *Legs*: fore tibia with single row of stout spines along anterior edge; hind tibia with 4 stout spines at outer apical rim; hind coxa angled at base but antero-ventral tooth not distinct. *Metasoma*: petiole distinctly arched at base in side view, dorsally rugose at base, acinose medially, striate apically; second tergum finely striate on basal 1/3–1/2, remainder

of terga smooth; ovipositor nearly twice as long as body.

*Male*.—Essentially as in female; hind wing with stigma-like swelling at junction of veins SC+R, r-m, R, and RS.

*Distribution*.—Occurs over entire eastern North America, Quebec to Florida, west to Ontario, Wisconsin and Texas.

*Biology*.—The only reliable rearing record is from *Magdalis olya* in hickory. It has also been associated with other cerambycids and clerids in hickory.

*Comments*.—This species is distinct with its small eyes and long malar space and very long ovipositor.

***Spathius trifasciatus* Riley**  
(Figs 19 A–G)

*Spathius trifasciatus* Riley 1873:106; Matthews 1970:66.

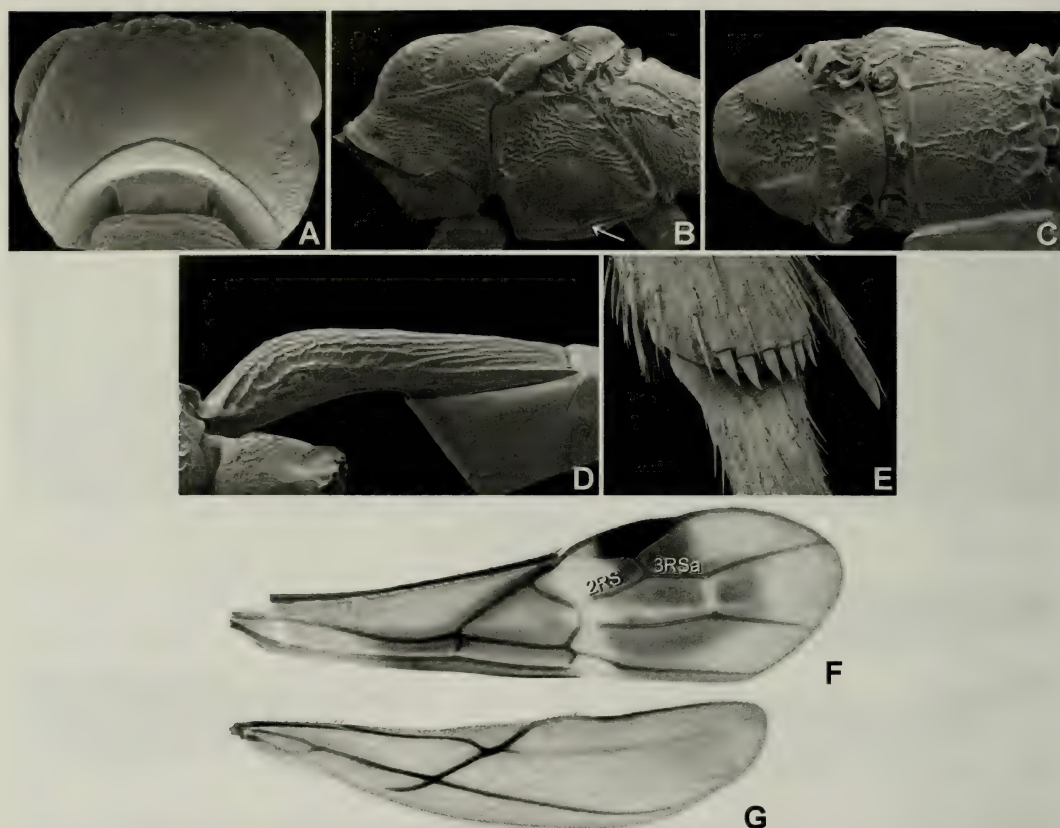


Figure 19. *Spathius trifasciatus* Riley, female. A, head dorsal view; B, mesosoma lateral view with carina along lower margin of sternalus indicated; C, mesosoma dorsal view; D, petiole lateral view; E, outer apical margin of hind tibia; F, fore wing with 2RS and 3RSa indicated; G, hind wing.

*Spathius unifasciatus* Ashmead 1893:70, 72. Synonymized by Muesebeck and Walkley 1951:170.

**Female.**—**Color:** body usually dark brown; head often honey yellow, scape, pedicel and basal third of flagellum honey yellow, remainder of flagellum brown; mesosoma occasionally light brown or honey yellow, mesoscutal lobes and propodeum always darker; petiole and metasomal terga 2–3 often honey yellow; legs often brown or honey yellow, tibiae with lighter band on basal 1/5; fore wings distinctly banded, basal 1/3 of stigma yellow, tegula usually yellow. **Body length:** 3.0–6.5 mm. **Head:** face transversely rugulose-striate; frons rugose, rugae usually transverse but occasionally longitudinal; vertex striate anteriorly diminishing to

smooth at occipital carina; temple finely striate, occasionally near eye and to malar space; vertex broad, ocellar-occipital distance about twice ocellar-ocular distance; temple nearly as wide as eye, in dorsal view bulging slightly beyond eye margin; malar space slightly less than 1/2 eye height; antenna with 25–37 flagellomeres. **Mesosoma:** propleuron transversely rugose, propleural flange smooth; pronotum carinate or porcate posteriorly, often rugose anteriorly, pronotal groove scrobiculate over pronotal collar; mesoscutal lobes strongly acinose, notauli strongly scrobiculate, meeting at scutellar furrow in deep triangular rugose area; scutellum acinose, scutellar furrow usually with 5 cross carinae; mesopleural disc longitudinally costate, the costae stronger dorsally, sub-



alar groove rugose; precoxal sulcus bordered below by distinct carina usually extending from epicnemial carina to mid coxa, several longitudinal carinae extending from middle of precoxal sulcus to mid coxa; propodeum rugose laterally, dorsal areas acinose, carinae not always distinct, areola transversely rugose or costate. *Wings*: fore wing vein 2RS longer than vein 3RSa, vein 3CU not interstitial with vein 1CU, thus small section of vein 2CU present; hind wing vein r-m about 1/3 length of vein 1M. *Legs*: fore tibia with several irregular rows of spines along anterior edge; hind tibia with 6–10 spines at outer apical rim; antero-ventral tooth at base of hind coxa sharply pointed. *Metasoma*: petiole distinctly arched in side view at base, rugose dorsally on basal half, costate on apical half; second tergum delicately striate or acinose at base; remainder of terga smooth and polished, occasionally with weak punctate band across terga anterior to setal band; ovipositor slightly longer than metasoma.

*Male*.—Essentially as in female except femora are more swollen and the fore tibia has fewer spines along the anterior edge.

*Distribution*.—Eastern U. S. from New York south to North Carolina, west to Wisconsin, Kansas and Texas.

*Biology*.—The only reliable records are rearings from *Scolytus quadrispinosus* Say (Coleoptera: Scolytidae) in hickory.

*Comments*.—The precoxal sulcus, which is bordered below by a distinct carina, is characteristic for this species and *brunneus* from which it can be separated by the longer ovipositor (longer than the metasoma in *trifasciatus*, shorter than the metasoma in *brunneus*), flat scutellum (swollen in *brunneus*), deeper area on mesoscutum where notauli meet, and darker color (mostly light brown to dark orange in *brunneus*).

#### COMMENTS ON THE BIOCONTROL OF THE EMERALD ASH BORER

Although species of *Spathius* have been reared from a variety of bark beetle

families, only a few are associated with *Agrilus* and other Buprestidae. Notes on these species are presented below.

*Spathius agrili* Yang (Figs 20A–H). This species was recently described from China (Yang et al. 2005) where it was reared from the emerald ash borer. Although only preliminary biological studies have been performed, it appears that this species is specific to the emerald ash borer and represents a very promising candidate for introduction into North America. *Spathius agrili* is similar to *S. leiopleuron* but differs in having the petiole in dorsal view narrower and the propodeum more closely sculptured than in *leiopleuron*.

*Spathius brunneus* Ashmead. This species has been recorded from *Agrilus fallax* as well as *Scolytus muticus* and is apparently not specific to buprestids.

*Spathius floridanus* Ashmead. This species has been reared from the buprestids *Agrilus anxius* and *A. bilineatus* (under the name *Spathius simillimus*) and *Chrysobothris femorata* and from several cerambycids and curculionids. More importantly, it has been reared from galleries of the EAB in Michigan. Thus, it represents the most promising North American species that could be utilized in a biocontrol program.

*Spathius* species. Among specimens reared in association with the emerald ash borer in Michigan were one female and three males of an apparently new species that does not accurately fit into the key presented above. The female will run to *impus* but has a longer ovipositor. Until further females of this species are obtained, we have decided not to describe it at this time. If it proves to be a distinct species, it will add one more possibility for the control of the emerald ash borer.

#### ACKNOWLEDGEMENTS

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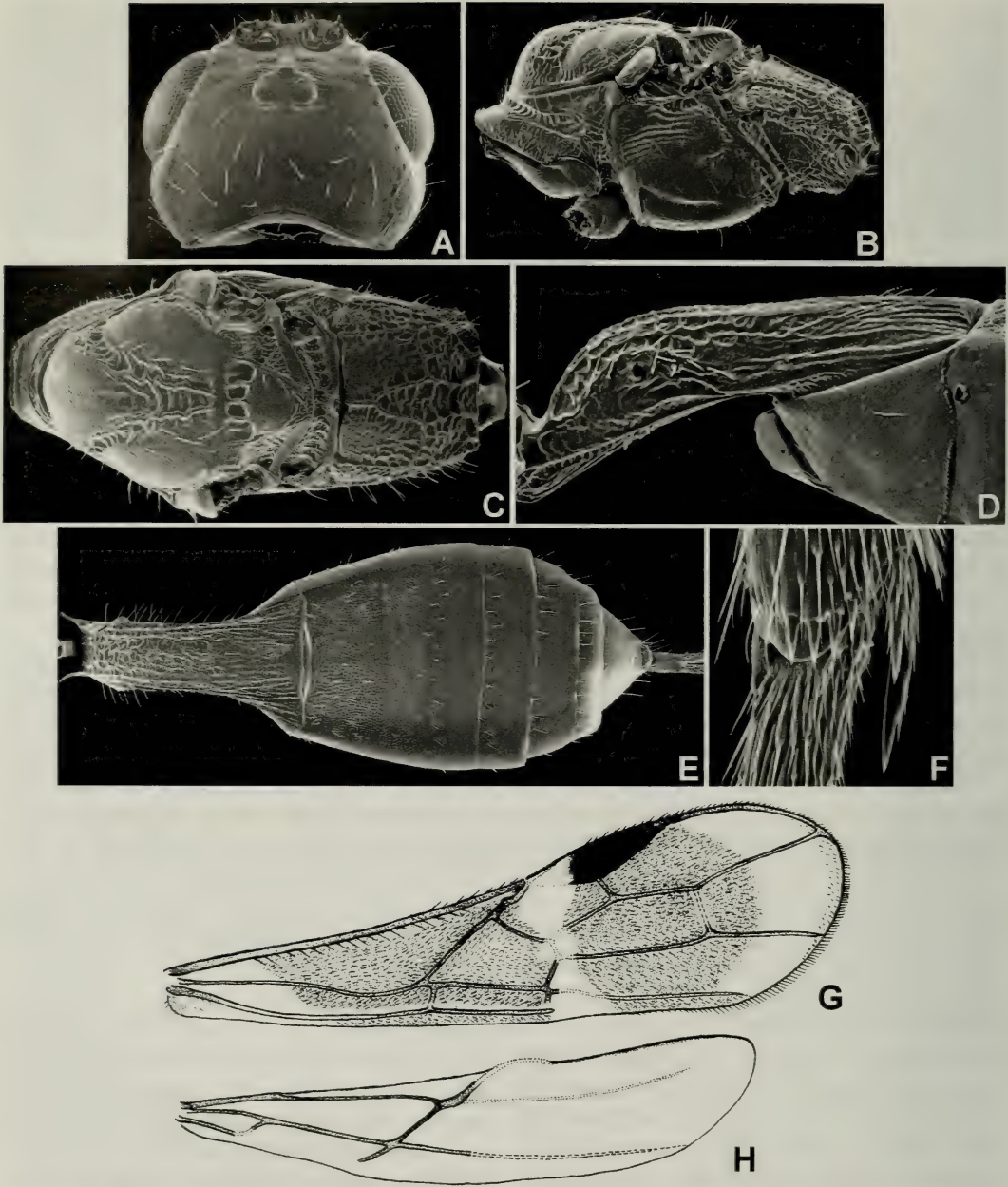


Figure 20. *Spathius agrili* Yang, female. A, dorsal view of head. B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma dorsal view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing. (Yang et al. 2005, used with permission.)

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## The Gyne of the Enigmatic Fungus-Farming Ant Species *Mycetosoritis explicata*

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**Abstract.**—We describe for the first time the gyne of the Neotropical fungus-farming ant *Mycetosoritis explicata*, a species hitherto known from only two workers collected in Goiás State, Brazil, in 1968. A redescription of the worker is presented. The likely non-monophyly of the genus *Mycetosoritis* and the possible position of the constituent species within the tribe Attini are discussed.

**Key words.**—Attini, *Mycetosoritis*, Myrmicinae, Neotropics, taxonomy

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*Mycetosoritis* Wheeler (Formicidae: Myrmicinae: Attini) is perhaps the most enigmatic of all fungus-farming ant genera. This taxon was erected by Wheeler (1907) as a subgenus of *Atta* Fabricius to accommodate the species *M. aspera* (Mayr) and *M. hartmanni* (Wheeler), and was raised to genus status by Creighton (1950). *Mycetosoritis* currently comprises five species: *M. aspera*, *M. clorindae* (Kusnezov), *M. explicata* Kempf (all southern South American), *M. hartmanni* (southern United States), and *M. vinsoni* Mackay (Costa Rica and Nicaragua). Emery (1906), Wheeler (1907), and Creighton (1950) all agreed that *Mycetosoritis* species combine characters otherwise found exclusively in either *Cyphomyrmex* Mayr or *Trachymyrmex* Forel. As pointed out by Kempf (1968), "... it must be admitted that this group, as defined by Emery (1922), is highly heterogenic."

Emery (1921, 1922) and Creighton (1950) did their best to list the characters uniting the species of *Mycetosoritis*, including: frontal lobes expanded and overhanging the clypeus (shared with most *Cyphomyr-*

*mex*); antennal scrobe complete (shared with the *Cyphomyrmex strigatus* species group; with *C. longiscapus* Weber, *C. muelleri* Schultz & Solomon, *C. wheeleri* Forel, and *C. costatus* Mann; and with some species of the *T. opulentus* group); and body hairs erect or curved, arising from tubercles at least on the gaster (shared with *Trachymyrmex* and *Acromyrmex*). The species *M. hartmanni*, *M. vinsoni*, and *M. clorindae* share with most *Cyphomyrmex* species an eroded sculpturing of the alitrunk and a generally smooth integument, whereas *M. aspera* and *M. explicata* share with many *Trachymyrmex* and *Acromyrmex* species a rougher integument punctuated by tubercles. For these and other reasons, we find it doubtful that the five species currently placed in the genus *Mycetosoritis* form a monophyletic group, except that *M. hartmanni* and *M. vinsoni* are clearly either sister species or conspecific. The polyphyly of *Mycetosoritis* is also supported by molecular phylogenetic data (Schultz and Brady 2008).

*Mycetosoritis explicata*, the focus of this paper, is exceedingly rare in collections, and its biology remains completely un-

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known. This species was described by Kempf (1968) based on two worker specimens. Besides these, only four other worker specimens are known to exist in collections. Herein we describe and figure the heretofore unknown gyne of this species. We also provide information about and figures of the poorly known worker caste. We conclude with a discussion of morphological characters relating the five species of *Mycetosoritis* to other members of the Attini.

## MATERIALS AND METHODS

Examination and measurement of specimens were completed at various magnifications using a Leica MZ16 light stereomicroscope and were recorded to the nearest 0.001 mm. Specimens were photographed using a JVC KY-F75U FireWire digital camera mounted on a Leica Z16 APO microscope with a Leica Motor-focus System attached to a Dell Optiplex GX620 computer, on which composite images were assembled using Auto-Montage Pro Version 5.03.0018 BETA software® (Synoptics Ltd.). Scanning Electron Micrographs (SEM) of uncoated specimens were taken using a Philips XL-30 ESEM with LaB6 under low vacuum conditions, gas pressure ranging between 0.7–0.9 Torr, and a backscatter detector. Images were cropped and enhanced using Photoshop CS2 Version 9.0.2® (Adobe Inc.).

## SYSTEMATIC TREATMENT

### Description

#### *Mycetosoritis explicata* Kempf

##### GYNE

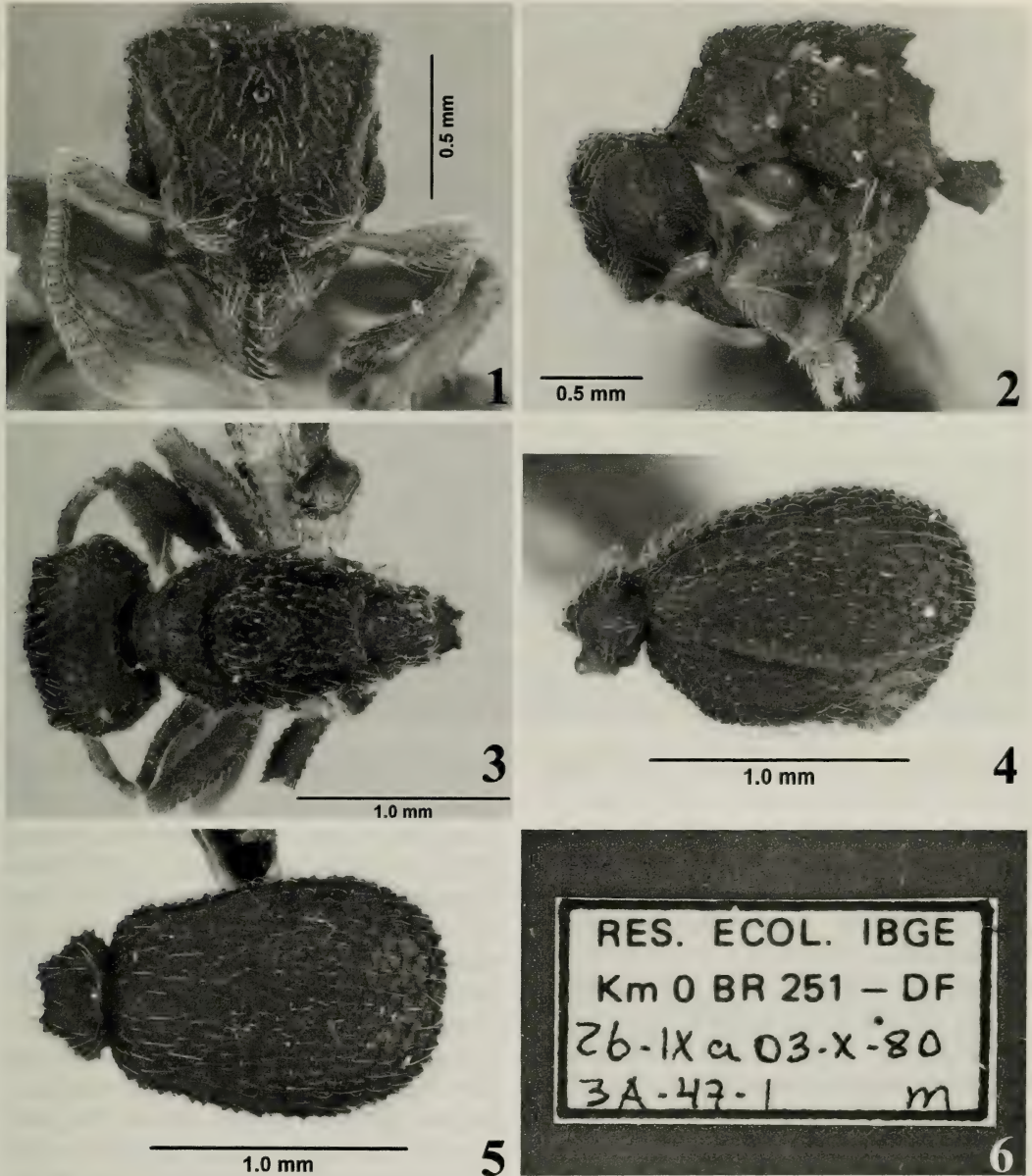
(Figs 1–7, 9, 10)

Label data: "Res. Ecol. IBGE; Km 0 BR 251 – DF; 26 ix a 03 x 80; 3A- 47- 1 m" (Referring to Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE), Distrito Federal - DF, Brasília, Brazil.) Measurements (in mm): Head

Length= 0.94; Head Width (excluding eyes)= 0.93; Mandible Length= 0.63; Weber's Length= 1.49; Scape Length (excluding the antennal condyle)= 0.64; Hind Femur Length = 0.99; Greatest Diameter of Eye = 0.23. Deposition: Reserva Ecológica IBGE, Brasília, Brazil.

*Head*.—In full-face view, head nearly as broad as long, posterior margin angulate at corners and impressed medially. Mandibles longitudinally striate and bearing 8 teeth, gradually increasing in size from the base. Clypeal apron broadly convex, the convexity interrupted medially by a conspicuous emarginate notch. A median seta (~0.16 mm in length) originates on the anteriormost edge of the clypeal apron, does not at all overlap the body of the clypeus, and extends across approximately one-fourth the length of the mandibles. Three pairs of lateral setae, long and simple and curved mesad, also originate on the clypeal apron. A pair of setal brushes, originating on clypeus below the frontal lobes, each consist of approximately 7–9 long setae and extend to one-half the length of the mandibles. Frontoclypeal teeth vestigial. Frontal lobes semicircular and greatly expanded, attaining the width of the head below the eyes (0.70 mm). Borders of the frontal lobes denticulate, imparting a serrated appearance. Frontal carinae produced into a denticulate lamina. Supraocular tubercle absent. Frontal carinae extending to posterior margin, there joining the subocular carinae to form a complete antennal scrobe. Antennal scape short, not exceeding the length of the scrobe. Anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex; posterior edge lacking denticles and bearing appressed hairs. Nuchal carina present and complete. Antennal scape in full-face view narrow in basal one-third, much broader in apical two-thirds, although slightly narrower at apex. Antenna 11-segmented, final segment approximately one-third the length of the flagellum. Eye with 14



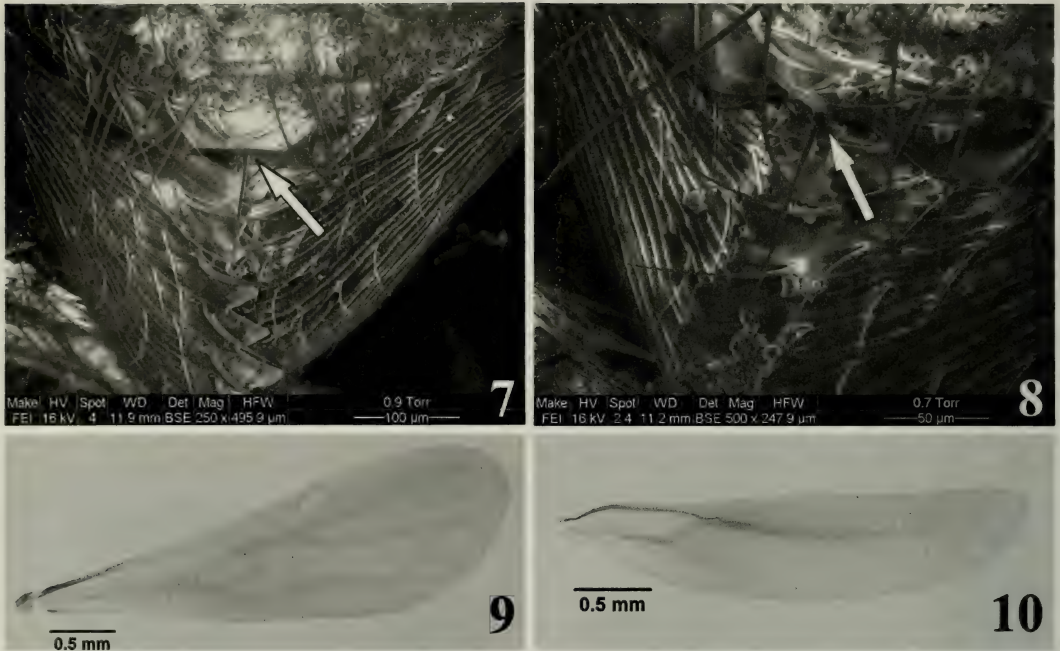


Figs 1–6. Gyne of *Mycetosoritis explicata*. 1, head, full-face view. 2, head, mesosoma, and petiole, lateral view. 3, head, mesosoma, and petiole, dorsal view. 4, postpetiole and gaster, lateral view. 5, postpetiole and gaster, dorsal view. 6, specimen label.

ommatidia across its greatest diameter. Three small ocelli present, distance between the posterior pair 1.3 times the maximum diameter of the eye.

*Mesosoma*.—Pronotum with a pair of short lateral tubercles connected by a conspicuous posterior pronotal carina,

most easily seen in frontodorsal view. Inferior corner of pronotum forming an obtuse angle, lacking a tooth or spine. Scutum without notable large divisions. Parapsidal lines distinct and raised, extending approximately half the length of the scutum. Axillae narrowly contiguous,



Figs 7–8. Scanning electron micrographs of the clypeal apron, showing the origin of the unpaired median seta, dorsal view. 7, gyne of *Mycetosoritis explicata*. 8, worker (paratype) of *M. explicata*.  
Figs 9–10. Wings of the gyne of *Mycetosoritis explicata*. 9, fore wing. 10, hind wing.

separated from scutellum by a broad, deep furrow. Scutellar process with a pair of posterior rounded teeth. Propodeal teeth short and obtuse. Propodeal spiracles small and directed posterad. Outer surface of tibia armed with a row of denticles not found on inner margin.

**Metasoma.**—Petiolar node approximately as long as broad, with a pair of tubercles on the posterior of the dorsum and several lateral denticles. Postpetiole wider than long; dorsum slightly concave, with lateral carinae; sides bearing several denticles; posterior margin vestigially emarginate. First gastral tergite (abdominal tergite IV) with pair of lateral carinae in anterior two-thirds; dorsum with small, pimple-like, piligerous tubercles which are connected to each other by rugae, forming an areolate surface sculpture. First gastral tergite longer than sternite, dorsally overhanging remaining segments. Terminus directed away and downward from longitudinal axis of body.

**Wings.**—Transparent, with minute hairs. Fore wing (length = 3.71 mm) with five

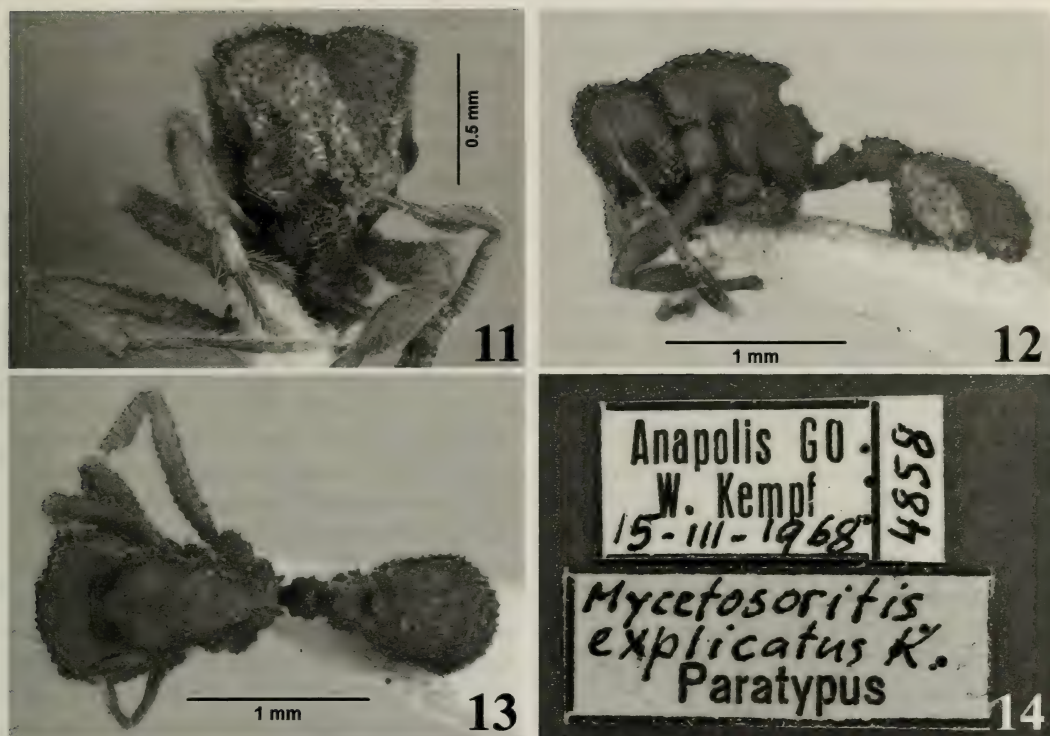
closed cells (terms follow Goulet and Huber 1993): costal (C), radial (R), cubital (Cu), first radial 1 (1R1), and first radial 2 (2R1); pterostigma small and pale (same color as veins); junction of cross-vein 1Cu-a and anal vein rounded, anal vein not extending past junction. Venation of hind wing (length = 3.08 mm) extremely reduced; seven hamuli on anterior margin.

Body color dark reddish-brown. Sculpture scabrous and areolate, particularly on scapes, legs, and gaster, due to the presence of scattered, pointed, piligerous pimples connected by irregular rugae. Hairs long, flexuous, and mostly strongly recurved, especially on clypeus, scapes, and gaster.

#### WORKER (Figs 8, 11–14)

Label data: "PARATYPE, BRAZIL, GO, Anapolis, W. Kempf, 15 iii 1968; 4858." This is the paratype specimen described in Kempf (1968) as "taken in the savannah





Figs 11–14. Paratype worker of *Mycetosoritis explicata*. 11, head, in full-face view. 12, body, lateral view. 13, body, dorsal view. 14, specimen labels.

south of the city of Anápolis, near Km 46 of the Goiânia-Brasília highway, Goiás State, Brazil, on March 15, 1968, W. W. Kempf leg. (WWK 4858)."

Measurements (in mm): Head Length = 0.80; Head Width (excluding eyes) = 0.80; Mandible Length = 0.48; Weber's Length = 1.20; Scape Length (excluding the antennal condyle) = 0.58; Hind Femur Length = 0.92; greatest diameter of eye = 0.16. Deposition: Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, Brazil.

#### Non-Paratypic material examined

1 worker, BOLIVIA, Santa Cruz, Perforación, 68 Km ESE Charagua, 11 xii 1993, 470 m, 19°55' S 62°34' W, ground forager, tropical dry forest, collector P. Ward. (PSW 12335-5). Deposition: Museum of Comparative Zoology (MCZC), Cambridge, Massachusetts, U.S.A. 1 worker, BRAZIL, Brasília, DF, UnB [Universidade de Brasília] Campus, 28 viii 1976, in Cerrado habitat, collector J.L.M. Diniz. (JLMD 1102).

Deposition: J. Diniz personal collection. 1 worker, PARAGUAY, Boquerón, Enciso, 3–6 xi 2001, 21°12' S 61°40' W, dry Chaco, sifted litter, collectors M. LePonce and T. Delsinne (#4075-41). Deposition: Alex L. Wild personal collection (ALWC). Specimen image examined at: <http://www.antweb.org/specimen.do?name=casent0173987&shot=p&project=worldants>

Characters and states similar to those of the gyne with the proper allowances for caste. Here we supplement the description of Kempf (1968).

*Head*.—In full-face view, head as broad as long. Mandibles triangular, inner margin with 8 teeth gradually increasing in size towards the apex. Eye with 10 ommatidia in the longest row. Median unpaired clypeal setae 0.09 mm long, originating on anteriormost edge of clypeus, a pair of lateral clypeal brushes consisting of 4–5 hairs each. Preocular carinae raised and extending backwards joining the frontal carinae at the occipital margin, forming a

complete antennal scrobe. Frontal lobes greatly expanded (0.59 mm). Nuchal carina present and complete. Anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex; posterior edge lacking denticles and bearing appressed hairs.

*Mesosoma*.—Dorsum of pronotum flat and with eroded sculpture or with some very small tubercles that bear some decumbent or subdecumbent hairs. Lateral margins of pronotum with a denticulate carinae. Lateral pronotal spine triangular and large. Lateral mesonotal tubercles large, triangular, and keeled. Posterior mesonotal lobes carinate. Dorsum of promesonotum forming a shield, carinate on all sides, separated from lateral portions of the promesonotum by abrupt right angles, and, posteriorly, overhanging and elevated above the propodeum. Basal lateral face of propodeum with carinules that end in small tubercles.

*Metasoma*.—Petiolar node approximately as long as broad, with a pair of dorsal bifid teeth. Postpetiole wider than long; sides bearing several denticles of similar length (differing from Kempf's [1968] description "... with a larger spine projecting from the middle of each side"); posterior margin vestigially emarginate. First gastral tergite (abdominal tergite IV) oblong, ovate, with pair of lateral carinae in anterior two-thirds; dorsum with small, pimple-like, piligerous tubercles which are connected to each other by weak but conspicuous rugae, forming an areolate surface sculpture. First gastral tergite longer than sternite, dorsally overhanging remaining segments. Terminus as in the gyne.

Body color ferruginous; gaster appears to be the same color (*contra* description in Kempf 1968). Color lighter than that of queen.

## DISCUSSION

The gyne and worker of *M. explicata* are clearly associated with each other by several compelling characters: a distinctive

microsculpture; the apical segment of the antenna large, as long as one-third the length of the flagellum; the frontoclypeal teeth either vestigial (gyne) or completely absent (worker); clypeal setal brushes present (consisting of 7–9 long setae in gyne or 4–5 long setae in worker); the anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex, the posterior edge lacking denticles and bearing appressed hairs; long golden hairs present on clypeus, scapes, and gaster; inferior angle of pronotum obtusely angulate; mandibles longitudinally striate and bearing 8 teeth; and outer surface of tibia armed with a row of denticles not found on inner margin. The gyne and worker differ in that the teeth on the posterior face of propodeum are short and tuberculate in the gyne, while more tooth-like in the worker; worker with a pair of bifid teeth on the dorsum of the petiolar node, whereas gyne with a pair of tubercles on the dorsum of disc of petiole; and color, being ferruginous in the worker and dark reddish-brown in gyne.

Since the creation of *Mycetosoritis* by Wheeler (1907), researchers have doubted the monophyly of *Mycetosoritis* and have disagreed about the phylogenetic positions of its constituent species. Wheeler (1907) stated that *Mycetosoritis hartmanni* "may be regarded either as a degenerate and simplified *Trachymyrmex* or as an aberrant *Cyphomyrmex*." Forel (1911) and Weber (1972) regarded *Mycetosoritis* as a primitive attine, transitional between *Cyphomyrmex* (considered by them to be the most primitive attine genus) and the remaining Attini. Forel (1912) placed the genus in one of two parallel attine "phyletic series," again as transitional between *Cyphomyrmex* and *Mycocepurus* Forel. Alternatively, Emery (1912), Wilson (1971), and Hölldobler and Wilson (1990) placed *Mycetosoritis* as closely related to the higher attines. The phylogeny of Schultz and Meier (1995) placed *M. hartmanni* as the sister group of the combined *Cyphomyrmex* and the higher



attines. Kempf (1964, 1968) compared *M. aspera*, *M. clorindae*, and *M. explicata* to members of the *Cyphomyrmex strigatus* group, based on the similar forms of the antennal scrobe, and implied that they may not be closely related to *M. hartmanni*. Of the genus *Mycetosoritis*, he states that "it must be admitted that this group, as defined by Emery (1922), is highly heterogenic. The type species *hartmanni* from Texas is quite distinct from the two South American species *aspera* and *clorindae* ..."

Our opinion is that *M. aspera* and *M. explicata* are more closely related to the higher attines (defined to include *Mycetagroicus*, *Trachymyrmex*, *Sericomyrmex* Mayr, *Acromyrmex* Mayr, and *Atta*), whereas *M. clorindae*, *M. hartmanni*, and *M. vinsoni* are much more distantly related to the higher attines. Based on molecular phylogenetic analyses (Schultz and Brady 2008), the latter two species are the extant representatives of a lineage that diverged early in the evolution of the Neoattini, prior to the origin of the common ancestor of *Cyphomyrmex* and the higher Attini. One morphological character that may link *M. aspera* and *M. explicata* to the higher attines is the reticulate sculpture, most notably on the gaster, shared with some *Mycetagroicus* Brandão & Mayhé-Nunes and some *Trachymyrmex* (e.g. *T. opulentus*) species. It is true, however, that the semicircular and greatly expanded frontal lobes constitute a character shared with most *Cyphomyrmex* species and that the complete antennal scrobe, formed by the frontal carinae extending to occipital corners and joining the subocular carinae, is a state shared with members of the *Cyphomyrmex strigatus* species group as well as with a subset of *Trachymyrmex* species, including those in the *T. opulentus* group. Obviously, the affinities of the five *Mycetosoritis* species remain enigmatic and will not be resolved until they are included in comprehensive morphological and molecular phylogenetic analyses. Such analyses, in turn, will only become possible when increased collecting corrects the exasperat-

ing rarity of specimens of *M. aspera*, *M. explicata*, and *M. clorindae*.

## ACKNOWLEDGEMENTS

We thank the collection of the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE), Jacques Delabie, and Roberto C.F. Brandão for loaning specimens; Eduardo Sanhudo and Jorge L.M. Diniz for useful information regarding the species; and Scott Whitaker (USNM) for assistance with the scanning electronic micrographs. This work was supported by National Science Foundation grants IRCEB DEB 0110073 to TRS and EF-0431330 to SGB and TRS. Additional funding was provided by the Ernst Mayr Travel Grant in Animal Systematics (Museum of Comparative Zoology) and the Jacob K. Goldhaber Travel Award (University of Maryland) to JSC. We are grateful to an anonymous reviewer for helpful comments on a previous version of the manuscript.

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#### NOTE IN PROOF

After submitting the final version of this manuscript, the authors received from Thibaut Delsinne (Royal Belgian Institute of Natural Sciences) 3 workers and 1 dealate gyne of *M. explicata* collected in Paraguay, Boqueron. The label information for these specimens is as follows. 1 gyne, PARAGUAY, Boqueron, Enciso, 4–5 xi 2001, 21°20' S 61°66' W, 400–590m trail, collector M. Leponce (sample ID code 4057; sampling point: T 89.02.0 r1; Winkler 24h; specimen ID code 7688). 1 worker, PARA-

GUAY, Boqueron, Enciso, 1–2 x 2002, 21°21' S 61°66' W, collector T. Delsinne (sample ID code 9911; sampling point: Q 120.07.0 r1; Winkler 24h; specimen ID code 11539). 1 worker, PARAGUAY, Boqueron, Enciso, 4–5 xii 2001, 21°20' S 61°66' W, 800–990m trail, collector M. Leponce (sample ID code 4109; sampling point: T 90.14.0 r1; Winkler 24h; specimen ID code 22851). 1 worker PARAGUAY, Boqueron, Nueva Asuncion, 1–2 xi 2001, 20°70' S 61°93' W, 0–190m dunes, collector M. Leponce (sample ID code 3897; sampling point: T 85.02.0 r1; Winkler 24h; specimen ID code 22959).



## BOOK REVIEW

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*Annotated catalogue of the Ampulicidae, Sphecidae, and Crabronidae (Insecta: Hymenoptera) of Turkey.* T. Ljubomirov & E. Yildirim. Pensoft, Sofia – Moscow. 2008. 316 pp. Price: €65. ISBN-978-954-642-312-2, ISSN 1312-0174

This is a summary of all published records on Turkish Sphecidae sensu lato, with the exception of two species for which no specific locality or province are available. The history of exploring and publishing on Turkish Sphecidae is presented, the oldest record being Lepeletier de Saint Fargeau (1845) and the latest from 2007. The authors follow the modern classification of the group and, like Brothers (1999) and Melo (1999), recognize the families Ampulicidae, Sphecidae, and Crabronidae (Heterogynaidae have not been collected in Turkey so far). For each species they provide a full bibliographic reference to the original description as well as an abbreviated (author, year, page, locality or province) reference to papers dealing with Turkish specimens (the number of publications cited is 138). What differentiates their work from similar catalogs are the distribution maps in Turkey provided for each species (the maps do not show individual localities, but provinces where the species have been found). Overall, this is an excellent tool for everybody interested in the Turkish fauna or in the systematics of Sphecidae s.l. An obvious conclusion from the book is that Turkey is an area of exceptional species richness, as 530 species have been recorded from the country (in comparison, Nemkov (2008) lists 344 species from the whole Asian part of Russia, and Blösch (2000) 248 species from Germany). Unfortunately, no Abstract is provided, and the two new synonyms by Ljubomirov, although discussed in the "About the Catalog" section, may be easily

missed by many readers, including Zoological Record: *Harpactus consanguineus* (Handlirsch, 1888) = *Harpactus transiens* A. Costa, 1887; and *Harpactus moravicus* (Šnoflak, 1943) = *Harpactus morawitzi* Radoszkowski, 1884. Lectotypes were designated by Ljubomirov for all four nominal species.

A few critical remarks are appropriate. First, the species *trichopygus* (de Beaumont) is surprisingly listed under *Brachystegus* rather than under *Synnevrus*. Second, for no apparent reason, the authors claim that the specific epithets in *Cerceris quadricincta*, *C. quadrifasciata*, *C. quinquefasciata*, *Oxybelus trispinosus*, *Prionyx lividocinctus*, and *Tachysphex albocinctus* are compounded nouns in apposition (not requiring agreement in gender), and that they ought to be spelled *quadricinctus*, *quadrifasciatus*, *quinquefasciatus*, *trispinosa*, *lividocincta*, and *albocincta*, respectively. This interpretation is incorrect: the prefixes tri-, quadri-, and quinque- are numerals, and the prefixes livido- and albo- are derived from the adjectives lividus and albus; the words fasciatus and spinosus are also adjectives, whereas cinctus is the passive perfect participle of the verb cingo (cingere). Therefore, the currently used spelling should be retained and not changed. Third, the spelling *Lithium jabojsi* is an incorrect original spelling and should be corrected to *jacobsi* (as required by Article 32.5.1 of the Code). Fourth, *Miscophus albufeire* is a minor misspelling of *albufeirae*. The authors, however, are right when they demonstrate that the correct original spelling is *Bembix portchinskii* Radoszkowski, not *portschinskii*, as misspelled by Handlirsch, 1893, and all subsequent authors. They also accept Baker's (1999) argument that Spinola's paper of 1805 (Faunae Ligusticae Fragmenta) was not a valid publication, they treat *Liris micans* (Spinola, 1806) as a

valid name for *Liris atratus* (Spinola, 1805), and the publication year for *Tachysphex nitidus* (Spinola) as 1806, not 1805. Baker's viewpoint, however, is controversial: he says that the Fragmenta were "privately printed for private circulation" and thus do not constitute a publication, but Passerin d'Entreves (1883) convincingly demonstrates the contrary.

WOJCIECH J. PULAWSKI

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**General Policy.** *The Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are acceptable if the species has economic importance or provides new data on the biology or evolution of the genus or higher taxon. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level. All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript. The language of publication is English. Summaries in other languages are acceptable. This journal is ISI-listed.

**The deadline for receipt of manuscripts is 1 September (for the April issue) and 1 March (for the October issue).**

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Upon **final acceptance** of a manuscript, the author should provide the editor with an emailed IBM formatted electronic version. CD-ROMs or 3.5 inch floppy disks are acceptable. Because symbols and tables are not always correctly translated it is best to also send a printed copy of the manuscript. Preferred word processing programs are Microsoft Word and WordPerfect. If possible, all words that must be italicized should be done so, not underscored. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double-spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. CDs and Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

Illustrations should be planned for reduction to the dimension of the printed page (14 × 20.5 cm, column width 6.7 mm) and allow room for legends at the top and bottom. Do not make plates larger than 14 × 18 in. (35.5 × 46 cm). Individual figures should be mounted on a suitable drawing board or similar heavy stock. Photographs should be trimmed, grouped together and abutted when mounted. Figure numbers should be on the plate. Include title, author(s) and address(es), and illustration numbers on back of each plate. Original figures need not be sent until requested by the editor, usually after the manuscript has been accepted. Reference to figures/tables in the text should be in the style "(Fig.1)" "(Table 1)". Measurements should be in the metric system.

Electronic plates may be submitted on disc, via email or uploaded to an ftp site (instructions will be given). They must be fully composited, labeled, and sized to fit the proportions of the journal page. Line art should be scanned at 1200 dpi (minimum input resolution is 600 dpi). Color or grayscale (halftone) images should have a dpi of 300-350. Color files should be in CMYK and not RGB. Graphics should be submitted as TIFF, Adobe Illustrator or EPS files. No PowerPoint or Word/WordPerfect files with images embedded in them are acceptable.

All papers must conform to the *International Code of Zoological Nomenclature*. The first mention of a plant or animal name should include the full scientific name including the authority. Genus names should not be abbreviated at the beginning of a sentence. In taxonomic papers type specimens must be clearly designated, type depositories must be clearly indicated, and new taxa must be clearly differentiated from existing taxa by means of keys or differential diagnoses. Authors are required to deposit all type material in recognized institutions (not private collections). Voucher specimens should be designated for specimens used in behavioral or autecological studies, and they should be deposited similarly. DNA sequences must be deposited in GenBank/EMBL/DNA Databank of Japan.

Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used, including discussion of program options used. A data matrix should be provided for morphological characters. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and reasons given for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

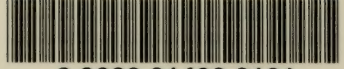
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